PhD Thesis

Federica Gemelli

The influence of phenotypic variation in a habitat-forming seaweed on intertidal gastropod communities

Supervisors:

Doctor Jeffrey T. Wright

Professor Craig Johnson

"Submitted in fulfilment of the requirements for the degree of Doctor of Philosophy (Fisheries Studies) "

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Declarations

Statement of originality

This thesis contains no material which has been accepted for a degree or diploma by the University or any other institution, except by way of background information and duly acknowledged in the thesis, and to the best of my knowledge and belief no material previously published or written by another person except where due acknowledgement is made in the text of the thesis, nor does the thesis contain any material that infringes copyright.

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Statement of co-author contributions

The thesis consists of two parts. The first part is an introduction to the topic and the ecological concepts behind my PhD project, with particular references to the outcomes of the research for the improvement of the current knowledge on the importance of seaweed species as ecosystem engineers in the marine intertidal.

The second part contains four data chapters (Chapter 2-5) which have each been prepared as peer-reviewed manuscripts. On all accounts, the experimental design and implementation, data analysis and interpretation, and manuscript development was the responsibility of the candidate and carried out in consultation with supervisory team and other third parties.
The following people and institutions contributed to the publication of work undertaken as part of this thesis:

Federica Gemelli, IMAS, University of Tasmania Candidate
Dr. Jeffrey Wright, IMAS, University of Tasmania Author 1
Prof. Craig Johnson, IMAS, University of Tasmania Author 2

Author details and their roles:
"Gastropod communities associated with different morphologies of the intertidal seaweed *Hormosira banksii*":
Located in Chapter 2
Candidate was the primary author and with author 1 and author 2 contributed to the conception and design of the research project and drafted significant parts of the paper
Candidate contributed approximately 60% to the planning, execution and preparation of the work for the paper. Author 1 contributed to the conception and design of the project and

drafted significantparts of paper. Author 2 conributed conceptual knowledge on the multivariate statistical methods and drafted the final draft of the manuscript.

We the undersigned agree with the above stated "proportion of work undertaken" for each of the above published (or submitted) peer-reviewed manuscripts contributing to this thesis:

Signed:_____ _____

	Supervisor: Dr Jeffrey T. Wright	A/Head of School: Dr Vanessa Lucieer
	School of Ecology & Biodiversity	School of Ecology & Biodiversity
	University of Tasmania	University of Tasmania
Date:	18/12/2018	18/12/2018

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Abstract

Canopy-forming seaweed are ecosystem engineers and play a central role in structuring entire communities through the amelioration of biotic and abiotic conditions and the provision of habitat. Their effects are particularly important in high-stress environments such as the intertidal zone where they provide the foundation for entire communities that would otherwise not occur there. Gastropods are among the most common group of invertebrates on intertidal rocky shores. Many species colonize seaweed canopies, or occur on the rock beneath the canopies, which reduce abiotic stress from strong wave action, high temperature, low humidity and provide a refuge from predation. While the importance of canopy-forming seaweeds as ecosystem engineers is recognised, the influence of morphological variation within intertidal seaweed species in traits such as thallus length, number and shape of structural elements on their engineering capacity and gastropod communities is not well understood.

Hormosira banksii (Turner) Descaisne (Fucales, Phaeophyceae) is one of the most abundant canopy-forming species on intertidal rocky shores in southern Australasia. As with many other intertidal seaweeds, *H. banksii* shows a large degree of morphological variation and several morphologies are recognized across coastal and estuarine environments. While this morphological variation is likely to reflect an adaptation to differences in the tidal regime and wave action at sites, whether morphology differentially influences engineering of abiotic factors and associated gastropod communities is not well understood.

This thesis examines variation in the structure of gastropod communities associated with distinct *H. banksii* morphologies and experimentally examines the evidence for a link between *H. banksii* morphology, amelioration of abiotic stress and gastropod abundance.

Chapter 2 is a large-scale descriptive survey of morphological variation in *H. banksii* and associated gastropod communities among multiple sites occurring in different habitats (coasts and estuaries), regions (east and north) and times (February-March and October-November), in Tasmania. Three seaweed morphs were identified on the north coast (small individuals), east coast (intermediate sized individuals) and in estuaries (large individuals). Each *Hormosira banksii* morph supported distinct gastropod communities with a small overlap in species and two dominant species were found in the different habitats. A slight correlation

occurred between *H. banksii* morphology and gastropod abundance, and thallus length, number and length of vesicles were the best predictors of the observed pattern.

Chapter 3 investigates variation of shell morphology of the two commonest gastropod species found within the canopies of *H. banksii* and the link between gastropod shell size and seaweed morphology. Large and small-scale differences occurred in shell morphology for both *Lunella undulata* (Lightfoot, 1786) and *Chlorodiloma odontis* (W. Wood, 1828). A different correlation occurred between the morphology of *H. banksii* and the shell morphology of gastropods, suggesting a species-specific influence of seaweed morphological traits, specifically thallus length and vesicle size, on the observed patterns.

Chapter 4 used two field experiments to explore the extent to which canopy cover and morphological variation of *H. banksii* influences engineering of key abiotic factors (temperature and irradiance) and colonisation by gastropod species. In the first experiment, canopy cover was manipulated to three levels (full [unmanipulated], half and quarter cover) and temperature, irradiance and gastropod abundance monitored. Despite any significative effect of canopy density on temperature and light levels, the full canopies supported the highest abundance of gastropods, with a species-specific colonization of the different sized canopies. In the second manipulative experiment, large (east coast) and small (north coast) morphs were transplanted to a single site and temperature, irradiance and gastropod abundance monitored for three months. The small morph of *H. banksii* lowered the temperature and irradiance under the canopies and supported the highest abundance of gastropods. Overall, there were weak correlations between temperature and light levels and gastropod abundance.

Chapter 5 used lab experiments to examine the habitat choice of the gastropod *Lunella undulata* and *Chlorodiloma odontis* and *H. banksii* for different morphologies (habitat quality) and biomasses (habitat quantity) at different temperatures. There was strong variation in species behaviour, highlighting the importance of *H. banksii* morphology and cover in buffering temperature and providing different microhabitats to intertidal gastropods.

Overall, this thesis has confirmed the importance of *H. banksii* as ecosystem engineer in the intertidal zone, supporting gastropod communities that differ between seaweed morphologies. However, the experimental tests of gastropod colonisation in the field and habitat choice in

the lab suggest the presence of small-scale and species-specific effects of *H. banksii* morphology and cover on gastropod abundance, highlighting the importance of *H. banksii* morphological traits in determining the bioengineer potential of this species across different habitat with different environmental conditions.

Chapter 1. Ecological community dynamics: from ecosystem engineering to community stability trough facilitation

Seaweeds play a major role in ecosystem functioning and provision of ecosystem services in the marine environment. As foundation species (*sensu* Dayton 1971), they are fundamental for the structure of marine ecosystems, providing habitat via the creation of canopies in which a large number of species found shelter (Steneck et al. 2002, Graham et al. 2007, Steneck and Johnson 2014) and food resources (Watanabe 1984; Orav-Kotta and Kotta 2004; Wright et al. 2014). Brown seaweeds of the order Fucales are among the most widespread and productive seaweed families and along with Laminariales and Desmarestiales, dominate temperate rocky reefs (Bertness et al. 1999, Christie et al. 2007, Bennett et al. 2016) but also occur in estuaries and even mangrove forests (Shepherd and Edgar 2013, Bennett et al. 2014). Thus, they can occur across a great range of environmental conditions (e.g. temperature, light, wave action and nutrients).

Canopy-forming seaweeds are able to modify abiotic conditions (for example they decrease water flow, temperature and irradiance), and the consequences of these modifications affect many other organisms. Foundation species that modify the environment in this way are now better known as autogenic ecosystem engineers (Jones 1994, 1997). The two concepts are synonymous (Angelini et al. 2011) but the second one became more popular over years, to refer to how different foundation species provide biogenic habitats to other species, and lead to abiotic and biotic changes which often provide favourable conditions for diverse associated communities. Despite the importance of the ecosystem engineer concept, understanding the strength and persistence of the engineer's activities within a system is important for understanding how it influences ecosystem dynamics (Reichman and Seabloom 2002; Wilby 2002). Indeed, the effects of ecosystem engineers vary in both time and space, and often depend on the background environmental variation (e.g. different temperature regimes, intertidal zones or wave exposures, Watt and Scrosati 2013; Scrosati and Ellrich

2018; Wright et al. 2018), as well as the density (Wernberg et al. 2005) and physical characteristics (e.g. shape, size, Chemello and Milazzo 2002; Christie et al. 2007) of the engineer itself at smaller scales.

By modifying the abiotic and biotic space, ecosystem engineers create or increase niches available to other species. The niche refers to the habitat occupied by a single species (Grinnel 1917). Each organism has a "fundamental niche" representing the physical space where a species can settle and develop self-sustained populations in absence of negative interactions (Grinnel 1917, Elton 1927, Hutchinson 1957). In contrast, the "realized niche" of a species includes not just the physical space occupied by the organism, but also interactions with other species, both positive and negative (Rodriguez-Cabal et al. 2012; Bulleri et al. 2016).

The role of negative species interactions in influencing the distribution and niche requirements of species were the basis of ecological studies for a long time, but more recently ecologists have included positive species interactions in community-level studies (Bruno et al. 2003; Bulleri et al. 2008; Angelini and Silliman 2014). Among these effects, facilitation, when one organism alters the environment positively influencing at least one other species, with neither of the two being negatively affected, is recognised as an important driver of community structure (Bruno et al. 2003; Bronstein 2009). Facilitative interactions have many potential beneficial effects because they can counteract the negative effects of biotic interactions and increase the realized niche of a species as well as ameliorate abiotic stress (Bruno et al. 2003; Stachowicz 2012). For example, species can persist in locations or situations which would otherwise be too stressful for the organism in the absence of facilitative interactions (Bulleri et al. 2016).

In the marine intertidal, where conditions are often highly stressful, habitat-forming invertebrates such as oysters, mussels and tubeworms (Underwood and Barrett 1990;

Borthagaray and Carranza 2007; Bracken 2018) and macrophytes such as seaweeds, seagrasses and mangroves have large effects on community structure (Larkum et al. 2016; Taylor and Cole 1994). Through the creation of canopies, they reduce physical stress by altering light, temperature and moisture regimes (Bertness et al. 1999; Watt and Scrosati 2013; Umanzor et al. 2017) and increasing environmental heterogeneity by providing microhabitats with different complexity (Chemello and Millazzo 2002). These modifications influence the amount of living space and resources available to other species and their effects, which often depend on the species characteristics (e.g. size and shape), result in an overall positive influence on diversity.

The importance and intensity of facilitation often increases as the background level of stress increases. For example, in the marine intertidal facilitation can increase with increasing tidal height (Bertness et al. 1999; Wright and Gribben 2017; Scrosati 2017), making intertidal canopy forming seaweeds an excellent study model to understand the importance of facilitation in regulating the community structure (Jenkins et al. 1999; Bulleri et al. 2012, Watt and Scrosati 2013a). However, despite the extensive body of research on facilitation by canopy forming seaweeds (Steneck et al. 2003; Wernberg et al. 2011), the degree of consistency in the effects of a single seaweed species in altering abiotic conditions for other species across habitats is not fully understood (see Watt and Scrosati 2013 as exception).

Important factors demonstrated to influence the facilitation of intertidal species include engineer characteristics such as density and morphology (Watt et al. 2013b). Indeed, the structural components (size, shape, surface texture) of primary habitat formers increase the heterogeneity and complexity (variety of refuge hole sizes, percentage live cover of seaweeds and hard substratum) of habitat structure. Habitat structure encompass several concepts including habitat heterogeneity, complexity and scale (McCoy and Bell 1991). The first two are quantitative and qualitative aspects of habitat (Stoner and Lewis 1985) referring

to the habitat size and the spatial area occupied by the structural elements of the habitat-former (e.g. branches), which influence the distribution of species through the increase of available living space and refuges from predation (Thompson et al. 1996). Both are scale-dependent (McCoy and Bell 1991; Taniguchi et al. 2003) since the effects of habitat complexity and the abundance of species vary depending on the scale at which they are measured.

Hypotheses about habitat complexity propose that in both terrestrial (Diehl 1992, Tews et al. 2004) and marine (Crowder and Cooper 1982; Susan 1997; Schagerström et al. 2014) ecosystems an increase in habitat structure (e.g. presence of canopies) provides more microhabitats and supports richer biological communities than simple habitats (e.g. bare rock). According to this hypothesis seaweed species with large surface area and finely branched thalli would host more invertebrate species than loosely branched algae (Dean et al. 1987; Chemello and Milazzo 2002; Christie et al. 2007), increasing the amount of living space and refugees provided (Heck and Thoman 1981; Crowder and Cooper 1982). However, there are exceptions to this pattern showing that the effects of seagrasses and seaweeds complexity (e.g. morphology, biomass) on invertebrate's abundance and richness can vary accordingly to the different species and community characteristics (Stoner 1982; Dean and Connell 1987).

Although the role of seaweeds as ecosystem engineers in the intertidal zone is well-established (Bertness et al. 1999; Hughes 2010), much of this work remains focused on the effects of a single species in a specific zone (Watt and Scrosati 2013; Scrosati and Ellrich 2018). As well, the capacity of seaweed engineer species to add physical habitat (e.g. creation of canopies by seaweeds) thereby increasing habitat complexity, will depend on the physical properties of the engineer (e.g. length, branching patterns and density of canopies). These have been evaluated across different species within a specific environment (Chemello and

Milazzo 2002; Umanzor et al. 2017) but there is little evidence of a change in the bioengineer potential of the same engineer species across different environmental conditions. It follows that for canopy-forming seaweeds showing different morphologies across different environments (e.g. *Fucus* Blanchette 1997, Wright et al. 2004; *Hormosira banksii* Macinnis et al. 2005; Mueller et al. 2015), it is necessary to consider the physical characteristics of each morph, when evaluating the facilitative effects of the engineer species on associated biotic communities.

Seaweeds **as ecosystem engineers in the intertidal zone**

Study species

Hormosira banksii (Turner, Decaisne) is an ecosystem engineer whose presence is important for the maintenance of a high diversity on intertidal rocky shores (Underwood et al. 1998; 1999; Lilley and Schiel 2006; Bishop et al. 2009; 2012; 2013; Hughes et al. 2014). This species is widespread on rocky shores in southeast Australia, including Tasmania, and New Zealand with an intertidal range (vertical extent between the lowest and highest tides) of ~ 0.6 metres (from ~0.7 m to 0.1 m), where it colonizes large areas and forms dense canopies offer shelter at low tide to many invertebrate species.

The phenotype of *H. banksii* is variable, resulting in the presence of distinct morphologies across coasts and estuaries characterized by different environmental conditions (Povey et al. 1991; Keough et al. 1998; Ralph et al. 1998; Schiel et al. 2004; Macinnis et al. 2005; Lilley and Schiel 2006; Mueller et al. 2015; Bishop et al. 2012, 2013; Coleman et al. 2018). Morphology can influence the abundance and diversity of molluscs associated with *H. banksii* which increase as the size of vesicles and thallus length increase (Bishop et al. 2009). However, there is no evidence that variability in morphology and density of *H. banksii* may affect the capacity of this species to buffer environmental conditions resulting in the

provision of different engineered effects for associated species. For this reason, the focus of this PhD thesis was to investigate the bioengineer potential of different *H. banksii* morphologies occurring on intertidal rocky shores and estuarine tidal flats and examine the role of seaweed morphology and canopy density in affecting the abundance, shell morphology and habitat choice of associated gastropod species.

The case study

The south-east coastline of Australia is dominated by rocky shores and is a global hotspot for seaweed diversity, with over 350 algal genera identified throughout the region (Kerswell 2006) and the highest seaweed diversity and number of endemic species (Underwood et al. 2007).

The Tasmanian coastline is characterized by intertidal boulder-fields from the north to the east and rock platforms in the south (Short 2006). Intertidal shores with boulders and cobbles are high dynamic environments due to the disturbance by waves and wind which increase the risk of dislodgement and desiccation. These shores can also be impacted by both natural (e. g. boulder movement from waves) or anthropogenic disturbances (e. g. trampling Keough and Quinn 1998 or increased nutrients, Bellgrove et al. 2010). Several seaweed species occur within the intertidal zone on these shores and *H. banksii* is often the most abundant. The morphology and density of *H. banksii* is highly variable between rocky shores and estuarine flats (Womersley 1967, Underwood 1999). A medium-length morph (standard) with cylindrical vesicles occur throughout much of Australia and New Zealand (Schiel 2004), while a longer morph with larger spherical vesicles occur in estuarine and mangrove ecosystems (large) (Osborn 1948, Bergquist 1959, Clarke and Womersley 1981, King 1981, Ralph et al. 1998, Macinnis-Ng et al. 2005). In addition, a short, bushy morph with tiny vesicles occurs on the north coast of Tasmania (Mueller et al. 2015). The different *H. banksii*

morphs provide habitat to a variety of species from epiphytic algae (*Notheia anomala*) to invertebrate species including hydroids (e.g. *Silicularia rosea*), sponges (e.g. *Haliclona sp*) and gastropods (e.g. *Lunella undulata*, *Chlorodiloma odontis*, *Phasianotrochus eximius*, *Cominella lineolata*), with the greatest abundance and diversity supported by *H. banksii* with large vesicles (Bishop et al 2009; 2013).

Understanding the potential effects of morphological variability in *H. banksii* on engineering of the environment and how these modifications affect the structure of the intertidal gastropod communities will extend knowledge about the fundamental role of this species as an ecosystem engineer and the importance of key traits in modifying the relationship with associated species. Thus, the overall aim of this thesis is to tease apart the effects of seaweed morphology on the structure of associated gastropod communities. The specific objectives of the four data chapters in this thesis are to:

(i) Examine the variability in *H. banksii* morphology and associated gastropod communities and the link between seaweed morphological traits and the abundance of gastropods across different habitats (coast and estuaries), regions (north and east Tasmania) and sites (three on the coast and two on the estuary within each region) (Chapter 2);

(ii) Examine the variation in the shell traits of the commonest gastropod species found associated with different *H. banksii* morphologies between the coast and estuary and explore the link between seaweed morphology and gastropod shell traits (Chapter 3);

(iii) Determine the bioengineer potential of different *H. banksii* morphologies and density in buffering temperature and light levels and facilitating gastropod abundance beneath the canopies on rocky shores (Chapter 4)

(iv) Examine the habitat choice of the two commonest gastropod species found associated with *H. banksii*, for different morphologies and biomass of *H. banksii* from the north and east coast of Tasmania.

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2 Chapter: Gastropod communities associated with different morphologies of the intertidal seaweed *H. banksii*

Abstract

Hormosira banksii is an important intertidal habitat-forming seaweed in southern Australia that shows large variation in morphology. We examined the relationship between morphological variation in *H. banksii* and associated gastropod community structure, abundance and diversity in Tasmania, southern Australia. We sampled both *H. banksii* and gastropods from sites in two habitats (coast and estuary), two times (February–March and October–November) at two regions (northern and eastern Tasmania). There were distinct *H. banksii* morphs on the north coast (small individuals), east coast (intermediate sized individuals) and in estuaries (large individuals). Multivariate analysis showed that gastropod communities varied among the different algal morphologies, and suggest an influence of morphological traits, specifically thallus length, vesicle number and size, on the distribution patterns of gastropod species. Despite the finding of distinct gastropod communities associated with the different *H. banksii* morphs, because the different morphs occur in different locations with different physical conditions, we cannot unequivocally attribute the differences in gastropod communities to seaweed morphology *per se*. Nonetheless, our results confirm that *H. banksii* is an important foundation species in the intertidal zone and suggest an influence of specific seaweed morphological traits on gastropods depending on the habitat in which they occur.

Introduction

The provision of biogenic habitat by foundation species (*sensu* Dayton 1971) or ecosystem engineers (Jones et al. 1994; 1997) is critical in determining the structure and functioning of communities (Menge and Branch 2001; Erwin 2008). In marine systems, organisms such as

seaweeds, seagrasses, molluscs, polychaetes and corals create habitat where other organisms find trophic and other resources and favourable conditions that reduce abiotic stress or predation (Bertness et al. 2001; Altieri et al. 2010; Wright et al. 2014).

Canopy-forming seaweeds are important bioengineers on rocky reefs (Steneck et al. 2002; Tuya and Haroun 2006) due to their capacity to ameliorate abiotic conditions for other species (Bruno et al. 2003; Veiga et al. 2013). The degree to which seaweeds facilitate associated species will be affected by background levels of environmental stress and the seaweeds' capacity to minimise it. In the marine intertidal, environmental stress can arise from high temperature, desiccation, wave exposure and light intensity (Davison and Pearson 1996). Seaweed morphology often differs among sites or regions depending on variations in these stressors (Chapman 1974; Cheshire and Hallam 1989; Blanchette et al. 2002; Fowler-Walker et al. 2006; Mueller et al. 2015). Variation in seaweed thallus size (habitat quantity), shape and branching (habitat quality), density and patch size will, in turn, affect engineering of local abiotic variables and have consequences for co-occurring species (Benedetti-Cecchi and Cinelli 1992; Crowe 1996; Schiel 2004). For example, dense patches of highly branched seaweeds are able to reduce wave energy and filter light, creating sheltered microhabitats for the colonisation and recruitment of other species (Whorff et al. 1995; Kelaher et al. 2001). Similarly, a higher number of structural elements (e.g. number of branches) is important for the creation of structurally complex habitats (Christie et al. 2007; Bishop et al. 2009), which provide more living spaces and refuges within canopies, supporting a high abundance and diversity of associated fauna (Crooks 2002; Bouma et al. 2009; Sueiro et al. 2011). Although variable structural complexity (habitat quantity and architecture) among algal species is known to affect the abundance of associated species (Veiga et al. 2014) and the structure of biological communities (Hansen et al. 2010), few studies have focused on how particular traits of a single species affect associated species (although, see Bishop et al. 2009; 2013).

Hormosira banksii Turner (Decaisne), hereafter *H. banksii*, is one of the most abundant intertidal species in southern Australia and New Zealand (Womersley 1967) and plays a key role in structuring intertidal invertebrate communities (Povey and Keough 1991; Keough and Quinn 1998; Schiel 2006). This species has a high resistance to thermal and desiccation stress (Schoenwaelder 2002; Kain 2015) and forms dense canopies that host a diverse assemblage of invertebrates (Schiel and Lilley 2007; Thomsen et al. 2016). Thinning of *H. banksii* canopies, for example from adverse environmental conditions (e.g. storms; Underwood 1998) and human disturbance (trampling; Keough and Quinn 1998), results in a decrease in the abundance and diversity of associated species (Lilley and Schiel 2006; Schiel and Lilley 2007, 2011). In addition, morphological traits, including the number of branches, the length and width of vesicles and thallus size, vary between different habitats (Ralph et al. 1998; Macinnis-Ng et al. 2005; Bishop et al. 2009; Mueller et al. 2015). In eastern mainland Australia, distinct morphologies occur on rocky shores and in estuarine mangrove forests, with the larger estuarine morph enhancing the abundance of some molluscs (Bishop et al. 2009).

In Tasmania, *H. banksii* also occurs in both coastal and estuarine habitats, and its morphology is highly variable with different morphs occurring in different regions (Mueller et al. 2015; 2018). On the north coast, which is exposed to a semidiurnal tidal regime, *H. banksii* has a small, highly branched thallus. In contrast, on the east coast, which has a mixed semidiurnal tidal regime, thalli are larger and the overall morphology is similar to that found on rocky shores of mainland Australia and New Zealand. As occurs in other parts of Australia (Ralph et al. 1998; Bishop et al. 2009), a large *H. banksii* morph occurs in estuaries in Tasmania attached to rocks and oyster shells. Previous studies have identified water movement (Ralph et al. 1998) and tidal regime (Mueller et al. 2015) as the best predictors of morphological variation in *H. banksii*. Although the size of the vesicles affects the abundance

and diversity of molluscs in New South Wales (Bishop et al. 2009; 2013), no studies have compared the possible effects of morphological variation in *H. banksii* on the structure of associated communities in Tasmania.

In this study we compared gastropod communities associated with different morphologies of *H. banksii* at sites in two regions of Tasmania (north and east), in each of two habitats (coast and estuary) and at two different times (February–March and October–November 2016). Specifically, we examined: (1) whether *H. banksii* morphology differs among region, habitat, time and site; (2) whether gastropod community structure, abundance, richness and diversity differ among region, habitat, time and site; and (3) the link between morphological variation in *H. banksii* and gastropod community structure.

Materials and methods

Sample sites

To assess the morphological variability of *H. banksii* and associated gastropod community structure, we conducted surveys at 10 sites in February–March (Time 1) and October–November (Time 2) of 2016. There were three sites on the open coast in both the north (Beechford (NC1), 41° 01’ 22” S, 146° 56’ 39” E; Bell Buoy Beach (NC2), 41° 02’ 23” S, 146° 49’ 56” E; and Greens Beach (NC3), 41° 04’ 41.8” S, 146° 45’ 35.8” E) and the east (Falmouth (EC1), 41° 30’ 50.2” S, 148° 16’ 39.0” E; Four Mile Creek (EC2), 41° 33’ 25.5” S, 148° 17’ 33.6” E; and Shelly Beach (EC3), 42° 34’ 0.5” S, 147° 53’ 17.5” E), and two estuarine sites in both the north (Clarence Point (NEs1), 41° 60’ 42.4” S, 146° 48’ 18.9” E; and George Town (NEs2), 41° 05’ 37.9” S, 146° 48.0’ 56.8” E) and east (St Helens (EEs1), 41° 20’ 18.2” S, 148° 16.0’ 3.7” E; and Orford (EEs2), 42° 31’ 05.6” S, 147° 54’ 03.9” E; see Fig. 2.1).

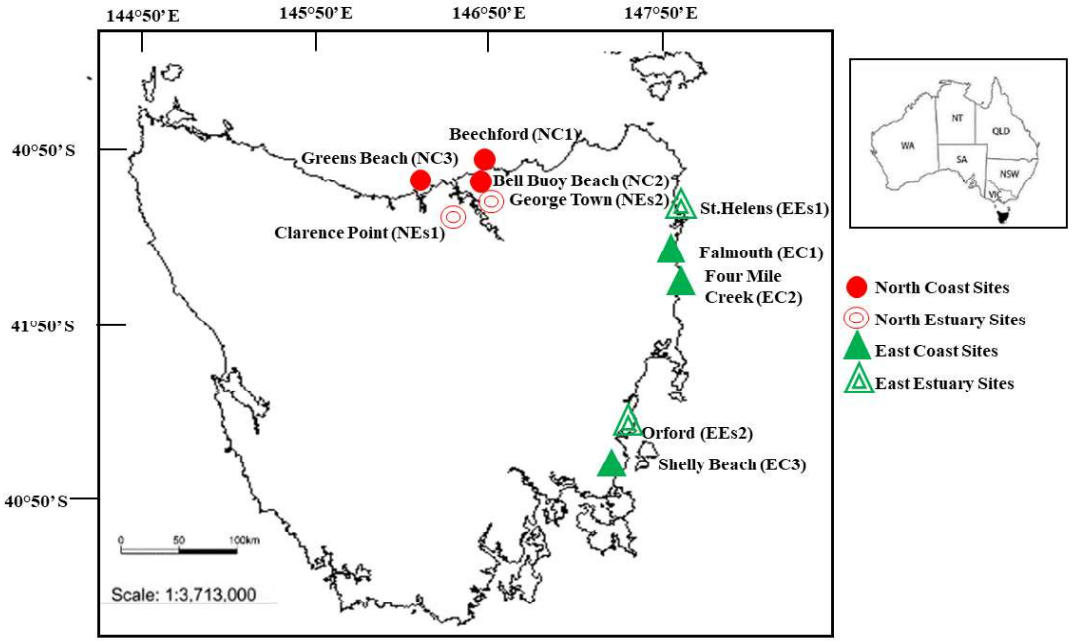

Fig. 2.1 Map of Tasmania showing the 10 sites (with abbreviations) sampled within 2 regions (north and east) and 2 habitats (coast and estuary). Qld, Queensland; NSW, New South Wales; Vic., Victoria; SA, South Australia; WA, Western Australia; NT, Northern Territory.

The northern coast of Tasmania is characterised by exposed cobble–basalt headlands with large intertidal boulder fields where *H. banksii* forms extensive beds in the low intertidal zones. The sites have low wave exposure and a semidiurnal tidal regime, which often leaves the organisms exposed to air twice a day (Mueller et al. 2015). *Hormosira banksii* on the north coast has a small bushy morphology, with individuals tightly packed and forming extensive canopies (Mueller et al. 2015). In contrast, the east coast is exposed to a semidiurnal or mixed semidiurnal tidal regime and stronger wave action, with adult *H. banksii* individuals growing larger than on the north coast. The estuarine sites are sheltered from wave action, and in estuaries in both regions *H. banksii* occurs attached to rocks or oyster shells (only at EEs1) on mudflats.

Values for wave exposure and mean temperature site were calculated or extracted as supporting information (Table A1, Appendix). For wave exposure we used the Baardseth Index (Baardseth 1970), a commonly used cartographic method to quantify exposure

(Ruuskanen et al. 1999, Wernberg and Thomsen 2005, Wernberg and Vanderklift 2010). This index considers wave effects from multiple directions and correlates well with wave height and maximum water velocity (Wernberg and Vanderklift 2010). To calculate the Baardseth Index we used a nautical chart (1:33333 scale), dividing adjacencies of each site into 40 sectors of an angle of 9˚. Sectors including skerries, islands, mainland shore or other obstacles within a fetch of 7.5 km were not counted. Thus, the resulting index refers to the sum of all the free sectors, where 0 represents complete shelter and 40 represents absolute exposure. Mean temperature values for each site at the two different sampling times were extracted from the Bureau of Meteorology website (BOM 2011) using the weather station closest to each site (Table A1 Appendix).

Sampling

At each site on each sampling occasion, twelve 50- x 50-cm quadrats were randomly placed on the shore 0.2–0.5m above the mean lower low water (MLLW) where *H. banksii* had 100% cover and with limited epiphyte cover. Quadrats with 100% cover were sampled to isolate the effects of morphology on gastropod communities. All gastropods within the quadrat (both in the canopy and on the rock beneath the canopy) were collected and fixed in ethanol for later identification to species level (or the lowest possible taxonomic unit) and enumeration. To analyse the morphological variability in *H. banksii*, within each quadrat one whole thallus (one to several fronds arising from the same holdfast) was randomply chosen and removed from the substratum using a butter knife (to avoid thallus breakage) and placed into a ziplock bag. Bags were filled with seawater and kept on ice until measurements were taken (1–2 days after collection). Samples were taken under a permit from the Institute of Marine and Antarctic Studies (IMAS), University of Tasmania, issued by the Department of Primary Industries, Parks, Water and Environment under the Living Marine Resources Management Act 1995.

Morphological variation in H. banksii

Hormosira banksii thalli comprise a small discoid holdfast with one to several fronds (first branches) arising from it. These fronds can differ in length and are made up of elongated, water-filled vesicles that vary in both length and width and are linked by short solid connectives (Osborn 1948; Bergquist 1959; Clarke and Womersley 1981; Macinnis-Ng et al. 2005; Mueller et al. 2015). More than one connective can arise from a vesicle, resulting in the creation of a different number of secondary branches (maximum of four from the same vesicle in the estuaries; F. Gemelli, pers. obs.).

To quantify the differences in morphology between site, region, habitat and time, we measured six morphological traits (as in Mueller et al. 2015) on each of 12 thalli (one per quadrat) from each site at each time, namely thallus length (i.e. the length of the longest frond measured from the tip of the holdfast to the longest branch), branching order (the highest number of branches arising from the holdfast), branching structure (the highest number of branching points available on primary branches), the total number of vesicles, vesicle length and width (measured using digital Vernier callipers to 0.05 mm). The branching order and branching structure were used to calculate the mean number of branches for each thallus and used as a measure of the overall complexity of each morph. Vesicle traits were measured on six healthy, unbranched vesicles, chosen at random on the thallus, to calculate the mean length and width for each sample. Finally, to determine biomass, each thallus was blotted dry with absorbent paper to remove excess water and weighed.

Data analysis

The significance of differences in *H. banksii* morphology were assessed using a multivariate analysis of variance (MANOVA) with the factors region (fixed, two levels, north v. east), habitat (fixed, two levels, open coast v. estuary), time (fixed, two levels, February–March v.

October–November) and site (random, three levels on the coast and two on the estuary) nested within combinations of region x habitat x time. In addition, each univariate trait of *H. banksii* (transformed as required based on λ values of Box–Cox plots to check homogeneity of variance) was analysed with a four-factor analysis of variance (ANOVA) with three fixed factors (habitat, region and time) crossed and one random factor (site) nested within the region x habitat x time interaction. Differences in *H. banksii* morphology based on six traits (thallus length, mean number of branches, total number of vesicles, vesicle length and vesicle width and wet weight) between regions (north v. east), habitats (coast v. estuarine) and time (February–March v. October–November) were displayed using a canonical analysis of principal coordinates (CAP) based on Euclidean distance after data were transformed (Box–Cox power transformation) to fix a left skewed distribution.

Gastropod abundance data were square root transformed to minimise the importance of the most abundant species and a matrix calculated based on Bray–Curtis distance. The differences in gastropod community structure were determined using a four-factor permutational multivariate analysis of variance (PERMANOVA, 9999 permutations) with the factors region (fixed, two levels, north v. east), habitat (fixed, two levels, open coast v. estuary), time (fixed, two levels, February–March v. October–November) and site (random, three levels on the coast and two on the estuary) nested within the habitat x region x time interaction. CAP was used to display the differences in gastropod community structure between regions (north v. east) and habitats (coast v. estuarine) at the different times (February–March and October -November). Finally, the spatial and temporal patterns of variation in gastropod abundance, species richness and Simpson's diversity within each quadrat were analysed with four-factor ANOVAs: with three fixed factors, region, time and one random factor (site) nested within the region x habitat x time interaction. Initially we

included *H. banksii* biomass as a covariate in these ANOVAs, but in all cases, it was not significant (as were interactions) and it was removed.

Linking H. banksii morphology and gastropod abundance

We assessed the extent of any relationship between the morphological traits of *H. banksii* and the abundance of gastropod species within the different habitats using two approaches. The morphological data for *H. banksii* were visualised through a Draftsman plot to check for any correlation between variables and whether the data were skewed and thus requiring transformation. All the variables were transformed because they were mildly left skewed. First, the BIOENV procedure from the PRIMER software package (ver. 6, K. R. Clarke and R.N.Gorley, PRIMER-E, Plymouth, UK) was used to identify the morphological variables that best correlate with the structure of the gastropod community as described by Euclidean distance. Second, a distance-based linear model (DistLM), with stepwise regression as selection criteria, was used to find the most parsimonious model of *H. banksii* variables predicting the patterns of gastropod abundance (Anderson et al. 2008). The Akaike information criterion (AIC) model (Akaike 1973) was used as a selection criterion, with smaller AIC values indicating the best combination of predictor variables (Anderson et al. 2008). The relationship between *H. banksii* morphological traits and gastropods was visualised through a distance-based redundancy analysis (dbRDA) based on Pearson's correlation. The dbRDA routine performed a constrained ordination of the abundance data using the DistLM model to explain the variation in gastropod abundance with a smaller set of predictor variables used to identify which *H. banksii* morphological traits had the strongest effect on the gastropod community.

Results

Morphological variation of H. banksii

There was significant variation in *H. banksii* morphology across region, habitat and time, as well as among sites (MANOVA; Table 2.1).

Table 2.1. Results of multivariate analysis of variance (MANOVA) testing the effects of habitat, region, time and site on the morphology of H. banksii on the coast and estuaries, Tasmania
Analyses were based on Euclidean distances on transformed data. Ha, habitat; Re, region; Ti, time; Si, site; Res, residuals; Ti(Si), the site is nested within the three main factors; Numd.f., degrees of freedom of the numerator; Den d.f., degrees of freedom of the denominator

Source	d.f.	Pillai	Approximate *F*	Num d.f.	Den d.f.	Pr(>*F*)
Ha	1	0.87	305.92	5	216	<0.0001
Re	1	0.82	200.26	5	216	<0.0001
Ti	1	0.56	55.18	5	216	<0.0001
Ha × Re	1	0.71	107.25	5	216	<0.0001
Ha × Ti	1	0.03	1.47	5	216	0.19
Re × Ti	1	0.45	35.69	5	216	<0.0001
Ha × Re × Ti	1	0.12	6.12	5	216	<0.0001
Ha × Re × Ti(Si)	12	1.45	7.52	5	216	<0.0001
Res	222					

The CAP plot revealed that the north coast *H. banksii* was clearly separated from the other regions and habitats, with the vectors for the former indicating a high degree of branching, a large number of vesicles and small vesicle size (Fig. 2.2). The east coast *H. banksii* was also largely separated from the estuarine *H. banksii* on both coasts. However, the north and east estuarine *H. banksii* showed a large degree of overlap, particularly in spring, which reflected the presence of large thalli with large vesicles (Fig. 2.2).

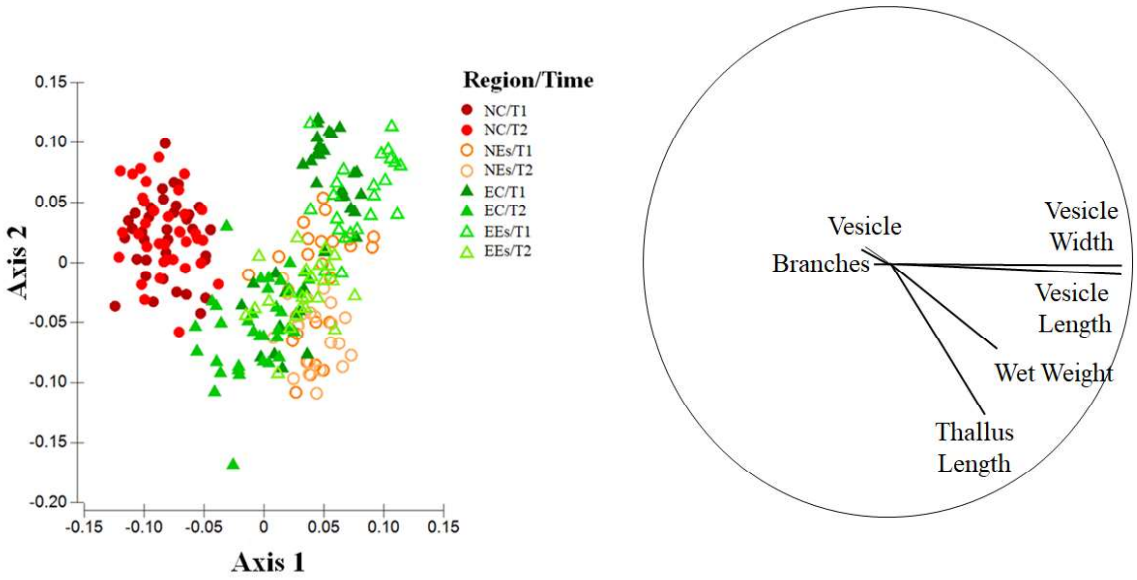

Fig. 2.2. Canonical analysis of principal coordinates (CAP) of six morphological traits of *H. banksii* across habitats (coast and estuary) and regions (east and north), at two times (February–March (T1) and October–November (T2)) pooled across sites for each habitat, region and time. NC/T1, north coast in February–March; NC/T2, north coast in October–November; EC/T1, east coast in February–March; EC/T2, east coast in October–November; NEs/T1, north estuary in February–March; NEs/T2, north estuary in October– November; EEs/T1, east estuary in February–March; EEs/T2, east estuary in October–November. Twelve thalli were sampled for each habitat, region and time.

Univariate analyses showed significant three-way interactions among sites within habitat, region and time for branches, vesicle number, length and width and wet weight ($P > 0.0001$). In contrast, minor differences occurred for thallus length ($P > 0.01$), which became bigger moving from the north coast towards the estuaries (Fig. 2.3).

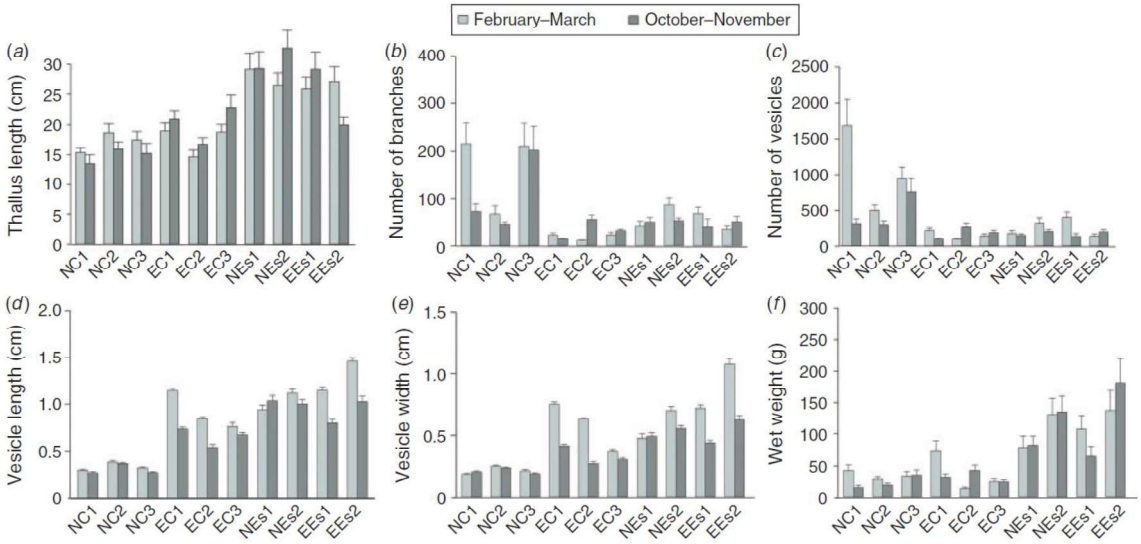

Fig. 2.3. Mean (± s.e.m.) values for six morphological traits of *H. banksii* sampled in two regions (north and east), two habitats (coast and estuary) at two times (February–March and October–November). There were three sites on the coast and two in the estuary for each region. Each column shows data from 12 thalli. NC1, Beechford; NC2, Bell Buoy Beach; NC3, Greens Beach; EC1, Falmouth; EC2, Four Mile Creek; EC3, Shelly Beach; NEs1, Clarence Point; NEs2, George Town; EEs1, St Helens; EEs2, Orford.

Gastropod community associated with H. banksii

There were 17 species of gastropods associated with *H. banksii*. Seven of these were found exclusively on the coast, three were found exclusively in estuaries and seven occurred in both habitats (Table 2.2).

Table 2.2. Gastropod species at each site (twelve 50- 3 50-cm quadrats) within each region (north and east) and habitat (coast and estuary) pooled across time. NC1, Beechford; NC2, Bell Buoy Beach; NC3, Greens Beach; EC1, Falmouth; EC2, Four Mile Creek; EC3, Shelly Beach; NEs1, Clarence Point; NEs2, George Town; EEs1, St Helens; EEs2, Orford (see Fig. 1)

Taxa	North Coast			East			North Estuary		East	
	NC1	NC2	NC3	EC1	EC2	EC3	NEs1	NEs2	EEs1	EEs2
Class Gastropoda										
Family Phasianellidae										
Phasianella australis	3	1	0	0	0	0	7	0	0	0
Family Trochidae										
Chlorodiloma odontis	27	70	193	11	2	1	48	27	0	0
Austrocochlea constricta	0	0	0	0	0	1	2	2	0	3
Austrocochlea porcata	0	0	0	0	0	0	0	9	12	582
Phasianotrochus eximius	2	6	1	0	0	0	1	0	0	0
Bankivia fasciata	0	0	0	1	0	0	0	0	0	0
Family Turbinidae										
Lunella undulata	40	74	48	207	200	9	0	0	0	0
Bellastrea aurea	0	0	20	0	0	0	68	0	0	0
Family Turritelidae										
Maoricolpus roseus	0	0	0	1	0	0	0	0	0	0
Family Cerithiidae										
Cacozeliana	0	0	0	0	0	2	0	0	0	0
Family Littorinidae										
Bembicium auratum	0	0	0	0	0	0	0	0	116	19
Family Ranellidae										
Cabestana spengleri	0	0	0	1	0	0	0	0	0	0
Argobuccinum pustulosum	1	3	0	0	0	0	0	0	0	0
Family Buccinidae										
Cominella lineolata	5	2	4	20	26	3	4	10	0	1
Family Nassariidae										
Nassarius pauperatum	0	0	0	0	0	0	0	2	0	1
Family Fasciolariidae										
Australaria australasia	1	0	0	0	0	0	0	0	0	0
Family Muricidae										
Dicathais orbita	0	1	0	0	3	1	0	1	0	0

The PERMANOVA revealed significant differences at all spatial scales, with most of the variation accounted for by site level variation (24%), followed by variation in habitats (12%) and region (12%), with 44% residual variation indicating the presence of both large- and small-scale variation (Table 2.3).

Table 2.3. Results of permutational multivariate analysis of variance (PERMANOVA) testing the effects of habitat, region, time and site on gastropod community structure Analyses were based on Bray–Curtis distances on square root transformed data following 9999 permutations of residuals under the full model. Ha, habitat; Re, region; Ti, time; Si, site; Res, Residuals; Ti(Si), the site is nested within the three main factors; R2, percentage contribution of each factor to the components of variation; MS, mean square.

Source	d.f.	MS	*F*	R^2	Pr(>*F*)
Ha	1	10.88	57.48	0.12	<0.001
Re	1	11.1	58.68	0.12	<0.001
Ti	1	1.28	6.78	0.01	<0.001
Ha × Re	1	4.21	22.24	0.04	<0.001
Ha × Ti	1	0.82	4.35	0.01	<0.001
Re × Ti	1	0.98	5.18	0.01	<0.001
Ha × Re × Ti	1	0.72	3.85	0.01	<0.001
Ha × Re × Ti(Si)	12	1.84	9.74	0.24	<0.001
Res		220	0.18	0.44	<0.001
Total		239		1	

The overall CAP analysis across habitats and regions showed very different communities of gastropods associated with *H. banksii* at those scales. The main species contributing to those patterns were *Lunella undulata* (Lightfoot, 1786) and *Chlorodiloma odontis* (W. Wood, 1828) on the coast, and *Bembicium auratum* (Quoy and Gaymard, 1834) and *Austrocochlea porcata* (A. Adams, 1853) in the estuary (Fig. 2.4).

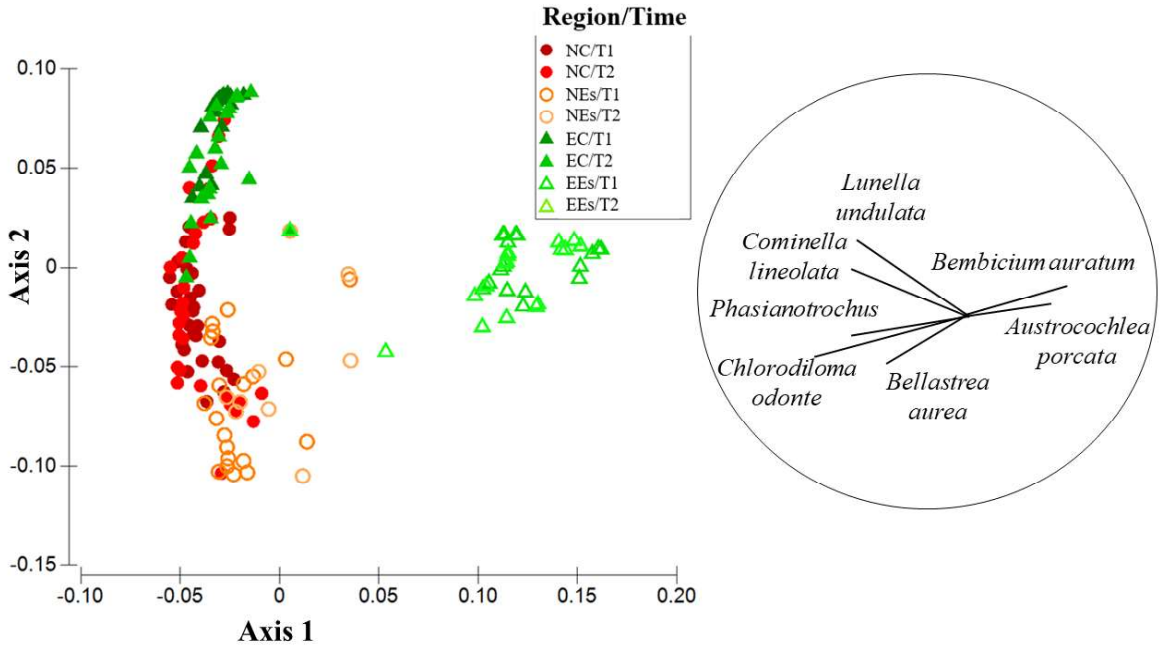

Fig. 2.4. Canonical analysis of principal coordinates (CAP) of gastropod species across habitats (coast and estuary) and regions (east and north), at two times (February–March (T1) and October–November (T2)) pooled across sites for each habitat, region and time. NC/T1, north coast in February–March; NC/T2, north coast in October–November; EC/T1, east coast in February–March; EC/T2, east coast in October–November; NEs/T1, north estuary in February–March; NEs/T2, north estuary in October–November; EEs/T1, east estuary in February–March; EEs/T2, east estuary in October–November. Twelve quadrats (50 x 50 cm) were sampled for each habitat, region and time.

There were significant three-way interactions among region, habitat and time (ANOVA, $P < 0.001$) for gastropod abundance, richness and diversity (Fig. 2.5).

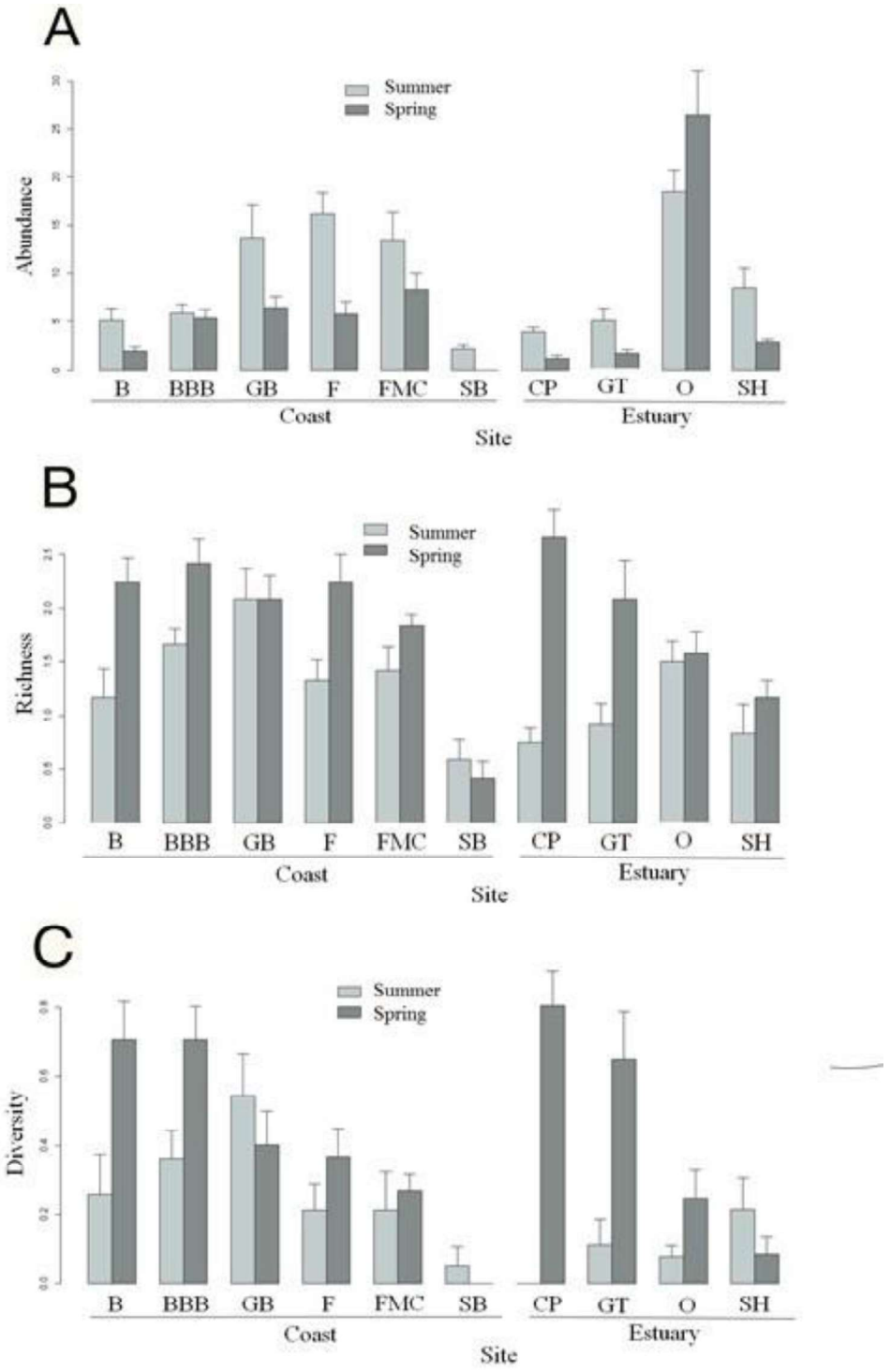

Fig. 2.5. (a) Gastropod abundance, (b) number of species and (c) diversity (Simpson diversity index), sampled in two regions (north and east) two habitats (coast and estuary) at two times (February–March and October–November). There were three sites on the coast and two in the estuary for each region. Data are the mean ± s.e.m. of 12 quadrats (50 x 50 cm). NC1, Beechford; NC2, Bell Buoy Beach; NC3, Greens Beach; EC1, Falmouth; EC2, Four Mile Creek; EC3, Shelly Beach; NEs1, Clarence Point; NEs2, George Town; EEs1, St Helens; EEs2, Orford.

Linking H. banksii morphology and gastropod abundance

All *Hormosira banksii* morphological traits were correlated with gastropod abundance, despite their contribution to the overall variation being low (Table 2.4).

Table 2.4. Distance-based linear model (DistLM) models. Marginal tests show the relative contribution of each variable tested individually. Conditional tests show best results for each number of variables fit into the model based on the Akaike information criterion (AIC).
Prop., proportion of explained variation for each variable; SS, sum of squares; R^2, amount of variation explained.

	SS (trace)	Pseudo *F*		*P*-value	Prop.
Marginal test					
Thallus length	66 004	18.94		0.0001	0.073
Mean branch	6030.2	1.61		0.12	0.067
Vesicle number	5691.6	1.52		0.14	0.063
Vesicle length	62 656	17.91		0.0001	0.069
Vesicle width	51 629	14.56		0.0001	0.057
Wet weight	62 715	17.93		0.0001	0.07
Conditional Test	SS (trace)	Pseudo *F*	AIC	*P*-value	Prop.
Thallus length	66 004	18.94	1959.3	0.0001	0.073
Vesicle length	19 304	5.64	1955.6	0.0001	0.021
Mean branch	13 084	3.87	1953.6	0.0009	0.014
Vesicle number	27 891	8.52	1951.5	0.0001	0.031
Vesicle width	11 682	3.61	1945.3	0.0015	0.01
	AIC	R^2		Number of variables	Selection
	1945.3	0.15		5	1–5

The BIOENV procedure identified thallus length and vesicle width as the best pair of variables correlated with gastropod abundance ($R^2 = 0.15$). The DiSTLM procedure selected the same three variables identified by BIOENV in the marginal test, plus wet weight. Among these, the conditional test reinforced the importance of thallus length, vesicle number and length in predicting the abundance of gastropods and indicated that the number of branches and vesicle width were also good predictors of the gastropods abundance ($R^2 = 0.15$, AIC = 1945.3) but not wet weight. The dbRDA (Fig. 2.6), using the best model identified by the

DISTLM, showed a separation between the coast and estuary along dbRDA1, reflecting the presence of different morphologies of *H. banksii* in the two habitats, in particular the larger vesicles in the estuaries, particularly in the east region. The number of vesicles was positively correlated with dbRDA2 (r = 0.36), whereas vesicle length and thallus length were negatively correlated with dbRDA1 (r = - 0.6 and - 0.5 respectively). This highlighted the importance of these three variables in separating the two habitats (coast and estuary) and affecting the number of gastropods.

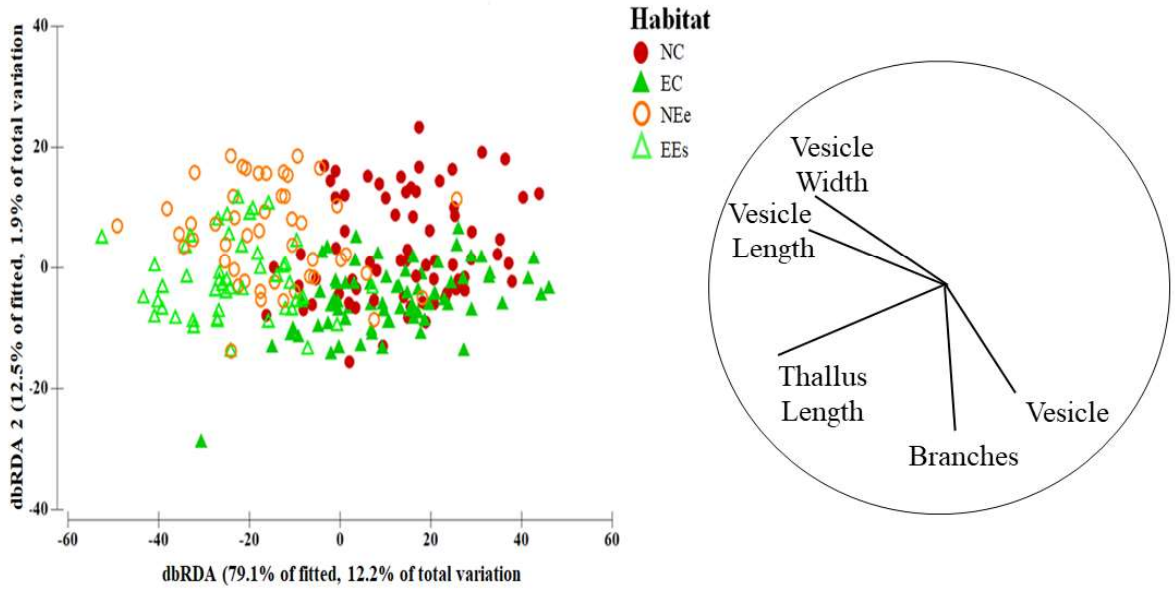

Fig. 2.6. Distance-based redundancy analysis (dbRDA) ordination for the relationship between *H. banksii* morphology and gastropod community pooled within regions (north and east) and habitats (coast and estuary) at each of three sites from each of the four regions (n =12 quadrats (50 x 50 cm) for each habitat and region). The inset shows the vectors based on Pearson correlation for *H. banksii* morphological traits that contribute most towards explaining overall and fitted variation with the dbRDA axes. NC, north coast; EC, east coast; NEs, north estuary; EEs, east estuary.

Discussion

The results of this study show distinct morphs of *H. banksii* occurring on the north coast, east coast and in estuaries, and these morphs support distinct communities of gastropods.

Although these regions and habitats are subjected to different environmental influences, and there was some overlap in species presence along with large spatial and temporal variations in gastropod community structure, the results highlight the potentially important role of seaweed morphology and thallus architecture (number of branches, vesicle length and width) in determining gastropod communities that use *H. banksii* as habitat.

Morphological variation of H. banksii

The presence of three different *H. banksii* morphs in Tasmania is consistent with previous findings for *H. banksii* around the coasts of Tasmania (Mueller et al. 2015) and across different environments (rocky shores and estuaries) in south-east Australia (Macinnis-Ng et al. 2005; Bishop et al. 2009; 2012; 2013; Kain 2015). Morphological variation has been described in many other fucoids, including *Fucus* (Blanchette 1997; Wright et al. 2004), *Sargassum* (de Paula and de Oliveira 1982) and *Durvillaea* (Cheshire and Hallam 1989). Morphological variation in seaweed can reflect local adaptation or plastic responses to environmental conditions. For *H. banksii*, the different morphs on the east and north coasts of Tasmania appear genetically fixed, with juveniles transplanted between coasts largely maintaining the morphology of their site of origin (R. Mueller, J. T. Wright and C. J. S. Bolch, unpubl. data; F. Gemelli, pers. obs.).

The main environmental factors suggested as important in causing the morphological variation for *H. banksii* are wave energy (Ralph et al. 1998) and tidal regime (Mueller et al. 2015). On the north coast of Tasmania, sites are exposed to higher tidal amplitudes and a semidiurnal tidal regime and, consequently, more stressful conditions at low tide for longer (Short 2006; Mueller et al. 2015), and *H. banksii* is small with a high number of branches and vesicles. This 'dwarf' morph of *H. banksii* has not been recorded in any other location around Australia or New Zealand. Smaller morphs of *Fucus distichus edentatus* and

Fucus gardneri occur in more wave-exposed sites on North American shores, where a size reduction prevents breakage or dislodgement due to high hydrodynamic forces (Sideman and Mathieson 1983; Dudgeon and Johnson 1992; Blanchette 1997). However, the north region of Tasmania has moderate wave exposure, suggesting wave energy is not driving this pattern; however, this region experiences long daytime low tides and high temperatures during summer (Mueller et al. 2015), which can increase thermal and desiccation stress. *Hormosira banksii* is susceptible to sunburn (Keough and Quinn 1998; Schoenwaelder 2002; Kain 2015), although it can recover from these effects unless the damage is too severe. The thick canopy formed by high densities of the small bushy morph is likely to create cooler, shaded conditions and reduce desiccation (Beermann et al. 2013; Scrosati and Ellrich 2018). Interestingly, a small morph of *F. gardneri* does occur in the very high intertidal zone at many low wave energy sites in the north-east Pacific where desiccation and thermal stress in summer is very high (Wright et al. 2004).

In comparison to the north coast, on the east coast of Tasmania wave exposure is higher and the tidal regime is mixed and mainly diurnal (Mueller et al. 2015). If shelter from wave action is a determinant of vesicle size, the east coast morph should have smaller vesicles than the north coast morph, but the opposite pattern was observed. The larger vesicles on the east coast may allow photosynthesis during light limitation. East coast sites are characterised by lower solar exposure compared with the north during summer (monthly light 4 kW m^2 in EC3 v. 4.6 kW m^2 in NC1), which may impair the photosynthetic performance (Chapman 1995) and therefore growth rate (Bell 1993, 1995).

Compared with *H. banksii* on both coasts, *H. banksii* in the estuaries had long thalli and large spherical vesicles. Low wave energy in sheltered estuaries and the reduced risk of breakage from waves compared with coastal environments has been suggested as allowing estuarine *H. banksii* to grow to a large size (Ralph et al. 1998; Macinnis-Ng et al. 2005). The

low wave energy, along with reduced salinity, in estuaries may also allow vesicles to become swollen and grow large (Burrows and Lodge 1951), and possibly reduce desiccation stress during low tide. The estuarine sites where we sampled were extremely sheltered, especially in the east region, and were exposed to the air for a long time during low tide.

Gastropod communities associated with different morphs of H. banksii

There was large spatial and temporal variation in gastropod communities. The size of marine habitat-forming species can affect facilitation of associated communities (Irving and Bertness 2009; Bishop et al. 2013), and the variable gastropod communities associated with different *H. banksii* morphs suggests morphology and thallus architecture may play an important role in this system. However, the large variation among sites and the low amount of variation in gastropod communities explained by morphological traits of *H banksii* (~15%) suggests environmental factors that differ among habitats, regions and sites are also likely to be important.

The distinct gastropod communities on the coasts versus estuaries reflected the high abundance of *C. odontis* and *L. undulata* on coasts (although *C. odontis* also occurred at the northern estuarine sites) and *A. porcata* and *B. auratum* in the estuaries (both were only found in that habitat). Previously, it has been shown that a large *H. banksii* morph found in New South Wales estuaries was colonised by higher numbers of gastropods than a smaller coastal morph (Bishop et al. 2009), and the very high abundance of *A. porcata* at EEs2 is consistent with that. However, the very different environmental conditions of coasts versus estuaries, including wave action, salinity fluctuations and amount of exposure at low tide, are likely to be crucial. Compared with the wave-dominated beaches and barrier estuaries in the east region, the northern coastal and estuarine sites are sheltered from the Australian mainland, with waves of ~1 m (Short 2006). The low wave exposure and semidiurnal tidal regime in this region may support species able to withstand long periods of emersion and

colder and hotter air temperatures during winter (June–August) and summer (December–February) respectively. Conversely, in the east region, the high hydrodynamic environment on the coast may limit the number of species due to the higher risk of dislodgement by waves.

The two coastal *H. banksii* morphs supported different gastropod communities, which may reflect the effects of the differences in thallus length and vesicle number and length, environmental factors or a combination of both. These morphs may create different microhabitats due to differential engineering of the abiotic environment (e.g. reduced temperature and desiccation, light intensity and wave action). The positive role of intertidal canopy-forming seaweeds in ameliorating harsh abiotic conditions for associated species is well documented (Bertness et al. 2001; Wright et al. 2014; Kay et al. 2016), as is the importance of a complex physical structure in providing different microhabitats (Christie et al. 2007; Loke and Todd 2016) and a wide range of niches for other species (Attrill et al. 2000). However, intertidal seaweed can also have negative effects on associated species (Cervin et al. 2004; Beermann et al. 2013). If facilitation by amelioration of abiotic stress by *H. banksii* is important in determining gastropod communities on the north coast, then the thick canopy formed by the small morph on the north coast, as well as the high number of vesicles and branches, may be important in facilitating certain gastropod species by reducing temperature, water loss and desiccation stress during low tide *C. odontis* was very abundant at sites on the north coast, where it occurred attached to the *H. banksii* or beneath its canopy. The higher abundance of *C. odontis* in association with the small *H. banksii* morph contrasts with the positive correlation found between the size of the vesicles and the abundance and diversity of gastropods in south-east Australia (Bishop et al. 2009). In contrast with *C. odontis*, *L. undulata* was more abundant on the east coast, where it was often found attached to *H. banksii* and in crevices covered by the seaweed. The overall higher abundance of gastropods in February when daytime temperature is higher reinforces the

hypothesis about an important protective role for *H. banksii* in ameliorating the abiotic conditions at low tide. Most of the gastropods associated with *H. banksii* are grazers, but the extent to which they feed on *H. banksii* is not clear. Intertidal gastropods graze on early lifecycle stages of *H. banksii* (Underwood 1998), but consumption of the macrothallus appears low and feeding scars were rarely observed on thalli in this study, further emphasising the important role of structural habitat for the associated species.

Similar to the coasts, in the estuaries *H. banksii* supported distinct gastropod communities across regions, with few species in common and different species dominant in each region. Because *H. banksii* morphology was similar in estuaries in both regions, with just small differences in the number and size of vesicles, the different community structure may be more related to the characteristics of the estuarine sites. In the north, both estuarine sites were near the mouth of the Tamar River estuary, where salinity is typically high (35 PSU), which may have allowed more oceanic species (e.g. *C. odontis*) to inhabit both coastal and estuarine habitats. In contrast, in the east, the estuarine sites were less exposed to oceanic conditions, with high freshwater input in winter (Edgar et al. 1999) and more estuarine species *A. porcata* and *B. auratum* dominant. *Austrocochlea porcata* is not strongly affected by habitat structural complexity within mangroves (Beck 1998), suggesting its high abundance at EEs2 may be more related to local environmental conditions.

The greatest numbers of *B. auratum* occurred attached to *H. banksii* vesicles or oysters beneath the *H. banksii* in St Helen's estuary. *Bembicium auratum* often occurs on sheltered intertidal muddy shores (Grove 2017), within oyster beds and attached to mangrove pneumatophores (Branch and Branch 1980; Underwood and Barrett 1990). The high abundance on oysters in the EEs1 estuary confirmed the positive effect of the oyster beds, which provide hard substratum for *B. auratum*, and suggests that *H. banksii* with large

vesicles and long thallus may provide additional living structure and favourable conditions (reduced
desiccation at low tide) for gastropod species within estuaries.

Conclusions

Overall, this survey confirmed the presence in Tasmania of three different morphs of *H. banksii*, each one supporting different gastropod communities with a small overlap in species occurrence.

Although this suggests a role of thallus morphology and architecture in providing different microenvironments, the present descriptive study is not able to separate the effects of morphology from larger environmental differences among regions, habitats and sites. Further experiments are needed to separate the roles of these factors in the patterns in gastropod communities observed herein.

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Chapter 3: Spatial patterns of abundance and shell morphology of two gastropod species associated with different morphologies of an intertidal seaweed

Federica Gemelli, Craig R Johnson and Jeffrey T. Wright

Abstract

Patterns of abundance and shell morphology of intertidal gastropods are typically thought to depend on environmental conditions but ecosystem engineers such as canopy-forming seaweeds can also influence the abiotic environment and thus, these traits. The intertidal seaweed *Hormosira banksii* is an abundant species on rocky shores and estuaries in south east Australia, where it creates thick canopies colonized by a range of invertebrates, particularly gastropods. In Tasmania (southern Australia), *H. banksii* shows large variability in thallus length and structure, with different algal morphologies on coasts and in estuaries. In this study, individuals of two gastropod species, *Lunella undulata* (Lightfoot, 1786) and *Chlorodiloma odontis* (W. Wood, 1828), were sampled from *H. banksii* at six sites within three different habitats (north coast, east coast and northern estuaries) to: (1) describe the spatial variability in their abundance and shell morphology, and (2) understand the linkage between *H. banksii* morphological traits and gastropod shell morphology. Gastropod abundance and morphology varied on large and small spatial scales and multivariate analysis suggested an influence of *H. banksii* morphological traits, particularly vesicle size, on these patterns. However, given that the two gastropod species use habitat differently (*L. undulata* occurs beneath the canopy while *C. odontis* occurs on the thalli itself), and that different *H. banksii* morphs occur in different locations, other factors need to be considered to fully understand the influence of seaweed morphology on these patterns. Nevertheless, our results show that the morphology of an ecosystem engineers may affect the abundance and morphology of associated species accordingly on environmental conditions at small scale.

Introduction

Invertebrates inhabiting the marine intertidal zone are subjected to varying intensities of environmental stress from both biological (e.g. predation) and physical (e.g. dislodgement by waves, temperature, salinity and desiccation) factors (Chapman 2000; Bates and Hicks 2005; Fraser et al. 2014). As a result, species such as gastropods have evolved adaptations (e.g. change in shell morphology, shell pigmentation, metabolic thermal regulation, behaviour) to their environment (Garrity 1984; Helmuth and Hofmann 2001; Bates and Hicks 2005). Abiotic and biotic habitat such as boulders, crevices and seaweed canopies can provide protection from these harsh conditions (Worthington and Fairweather 1989; Bulleri et al. 2002; Cartwright and Williams 2012). In the case of seaweed canopies, variation in their density or morphology can influence the abundance and the morphology of intertidal invertebrates (Chemello and Milazzo 2002; Smoothey 2013; McAbendroth et al. 2005).

Canopy-forming seaweeds are ecosystem engineers (*sensu* Jones 1994, 1997) and create complex, three-dimensional habitat where temperature and desiccation stress are lower for small invertebrates at low tide (Bertness et al. 1999; Wright et al. 2014; Jurgens and Gaylord 2018; Scrosati and Ellrich 2018). Studies comparing between seaweed species show that seaweeds with a complex thallus architecture (e.g. long thalli, high number of branches and vesicles) increase the abundance and morphology of associated species (Gee and Warwick 1994, Beck 1998; Hooper and Davenport 2006, Bates and DeWreede 2007; Veiga et al. 2014; Schagerström et al. 2014). As well as thallus architecture, the ability of seaweed to provide favourable conditions for associated species can change according to the background environmental conditions (Beck 1998, Kelaher, 2007). For example, on medium to high wave-exposed shores, where gastropods shells tend to be relatively small with large apertures, providing a relatively large foot which increases attachment strength (Underwood and McFadyen, 1983; Trussell et al. 1993; Boulding et al. 1999), species colonize more

structured (e.g. *Corallina officinalis*, *Hormosira banksii*) than unstructured habitat (e.g. bare rock, crevices), where relatively large gastropods occur (Worthington and Fairweather 1988; Smoothey 2013).

Despite the evidence of differences in the abundance and shell morphology of gastropod species associated with canopy-forming seaweed of different structural complexity, the mechanisms for these effects are not often clear. More complex seaweed with a great number of branches and vesicles may provide greater protection against wave action than large flat species (Tuya et al. 2008), and in the intertidal, may reduce temperature beneath the canopies compared to adjacent open substratum (Bertness et al. 1999; Jones and Boulding 1999). In comparison to studies between different seaweed species, relatively few studies have explored the relationship between morphological variation in a single seaweed species and gastropod abundance (although see Bishop et al. 2009; 2012; 2013, Gemelli et al. 2018) and shell morphology (largely size) of associated gastropod species (Worthington and Fairweather 1989; Smoothey 2013). Given the widespread morphological variation within seaweed species (e.g. *Fucus* Wright et al. 2004; *Hormosira banksii* Macinnis-Ng et al. 2005), and the potential for different seaweed morphologies to provide different sub-canopy microenvironments, understanding the link between seaweed morphology and shell morphology of associated gastropods is an important step in understanding the potential adaptive responses in these gastropods to differing abiotic conditions engineered by seaweed.

Hormosira banksii is one of the most abundant canopy-forming seaweeds on intertidal shores of temperate Australasia due to its tolerance of high temperatures and desiccation (Schoenwaelder 2002; Kain 2015). This species creates complex three-dimensional habitats, where a variety of species find shelter beneath the canopy, particularly at low tide (Povey and Keough 1991, Keough and Quinn 1998, Lilley and Schiel 2006; Schiel 2004; Schiel and Lilley 2011; Gemelli et al. 2018). As with many other brown

seaweeds (e.g. *Fucus* sp. Sideman and Mathieson 1983; Blanchette 1997 and *Ecklonia* Mabin et al. 2013), *H. banksii* shows a large degree of variability in morphological traits and manifests different seaweed morphs on rocky shores of the open coast and estuaries in southeast Australia (Ralph et al. 1998; Macinnis et al. 2005).

On Tasmanian intertidal shores, the morphology of *H. banksii* varies among habitats (coasts vs. estuaries), regions (north, east and west coasts), and among sites within these regions (Mueller et al. 2015; Gemelli et al. 2018). There is a small bushy morph that only occurs on the north coast, an intermediate sized morph on the east and west coasts and a large morph (much longer thallus and larger vesicles) which occurs in estuaries (Mueller et al. 2015; Gemelli et al. 2018). The different *H. banksii* morphs found on the coast and in estuaries support different gastropod communities (Gemelli et al. 2018), with a small overlap in species distribution. The Turbo *Lunella undulata* (Lightfoot, 1786), a commercially harvested species (Ab Lah et al. 2016) and the Trochid *Chlorodiloma odontis* (Wood, 1828) are the most common species found within *H. banksii* canopies in Tasmania. *Lunella undulata* is often found under the canopies on coasts, while *C. odontis* occurs attached to the vesicles of *H. banksii* on both coasts and in estuaries (in northern Tasmania) with peaks in abundance in summer (January-February, Gemelli et al. 2018). In addition, while previous studies have shown that the presence of *H. banksii* enhances the abundance and diversity of invertebrates (Bishop et al. 2009; Hughes et al. 2014) and that larger estuarine thalli support more mollusc species than rocky shore thalli with smaller vesicles (Bishop et al. 2009; 2012), no studies have investigated the possible link between *H. banksii* morphology and the shell morphology of gastropods which use the canopies as habitat.

Here we determine patterns of spatial variability in the abundance and shell morphology of *L. undulata* and *C. odontis* at different sites in two regions (north and east) and habitats (coast and estuary) at different times (February-March and October-November

2016). Specifically, we conducted a mensurative experiment to: 1) determine whether abundance and shell morphology of *L. undulata* and *C. odontis* varied among different morphologies of *H. banksii*, and 2) explore the link between *H. banksii* morphology and gastropod morphology.

Materials and Methods

Sampling and Study Sites

To assess the variability in *H. banksii* morphology, abundance and shell morphology of *Lunella undulata* and *Chlorodiloma odontis,* we conducted surveys during the austral summer/autumn (February-March (T1)) and spring (October-November (T2)) 2016. We aimed to collect the two gastropod species from two regions (north and east) in Tasmania, in two habitats (open coast and estuary), and from two sites for each region and habitat combination. However, *L. undulata* was not found in estuaries and *C. odontis* was not found in estuaries in the east (Gemelli et al. 2018) and so used different sampling designs for each species (Fig. 3.1). *Lunella undulata* was sampled from two sites on the north coast (Bell Buoy Beach, north coast 1 (NC1) 41°02'23"S, 146°49'56"E and Greens Beach (north coast 2 (NC2) -41°.04'41.8" S, 146°45'35.8" E) and east coast (east coast 1, Falmouth (EC1) 41°30'50.2" S, 148°16'39.0" E and Shelly Beach (east coast 2 (EC2) 42°34'00.5 "S, 147°53'17.5" E). *C. odontis* was sampled from the same coastal sites as well as two northern estuarine sites (Clarence Point, north estuary 1 (Nes1) 41˚06'42.4" S 146 ˚ 48'18.9" E and George Town, north estuary 2 (Nes2) 41˚05'37.9" S 146 ˚ 48'56.8" E) (Fig. 3.1).

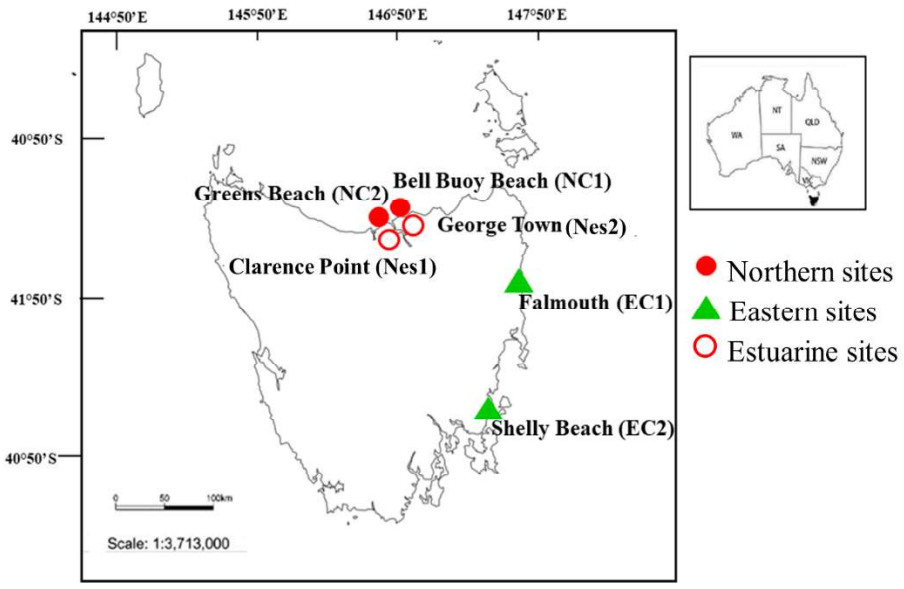

Figure 3.1. Map of Tasmania showing the 6 sites (with abbreviations) sampled within 2 regions (north and east) and 2 habitats (coast and estuary). Qld, Queensland; NSW, New South Wales; Vic., Victoria; SA, South Australia; WA, Western Australia; NT, Northern Territory.

Northern sites have a lower wave exposure (see Table A1 in the Appendix) than the eastern sites and a semidiurnal tidal regime leaving the organisms exposed to the air twice each day (Mueller et al. 2015). The small bushy *H. banksii* morph occurs on the north coast, with individuals typically packed tightly together to form dense canopies that are often exposed to high temperatures and strong winds at low tides (F. Gemelli personal observations). In comparison, eastern sites have a semidiurnal or mixed semidiurnal tidal regime, with the site in the northeast (EC1) more exposed to wind-driven waves than the site in the southeast (EC2, F. Gemelli personal observations). In the east, a longer, less branched *H. banksii* with bigger, cylindrical vesicles occurs, with canopies less exposed to the air but exposed to stronger wave action. In contrast, the estuarine sites in the north are sheltered from wave action, allowing *H. banksii* to reach a large size. At these estuarine sites, *H. banksii* are attached to rocks on the sandy tidal flats to form interspersed patches along the shore.

To determine the morphological variation of *H. banksii*, we sampled one whole seaweed thallus from twelve 50 x 50 cm quadrats placed randomly at each site where *H. banksii* had ~100% cover and was free of epiphytes. Sampling was done during the daytime at approximately 0.5 m above the mean lower low water (MLLW). Within each quadrat, we also collected all *L. undulata* and *C. odontis* to determine their abundance and morphology. When less than 40 individuals of a species were collected at a site (if present), we collected more individuals for each species to have sufficient numbers to examine variation in shell morphology. All the biological material was placed in ziploc bags, transported to the laboratory and kept on ice until measurements were taken (1-2 days after the collection).

Morphological variation in H. banksii

Hormosira banksii thalli have a small discoid holdfast which provides attachment to hard surfaces such as rocks and bivalve shells. One to several fronds arise from the holdfast (1st branches). Fronds are made up of elongated fluid filled vesicles, variable in size, and linked by short solid connectives. From each vesicle arise a different number of connectives which result in the creation of secondary branches.

To assess the morphological variation of *H. banksii*, we measured six morphological traits as an estimate of the overall size and complexity of the seaweed on each of the 12 thalli. These were *viz.*: thallus length (length of the longest frond measured from the tip of the holdfast to the longest branch); branching order (the highest number of branches arising from the holdfast); branching structure (the highest number of branching points available on primary branches); total number of vesicles and vesicle length and width (measured with digital Vernier calipers to 0.05 mm). As a measure of thallus complexity for each morph we summed up the branching order and branching structure values and divided the result by two, to calculate the mean number of branches. Vesicle traits were measured on six randomly selected healthy, unbranched vesicles, to calculate the mean length and width for each thallus.

The differences in *H. banksii* morphology were analysed with a 3-factor permutational multivariate analysis of variance (PERMANOVA), with the factors habitat (fixed, three levels, north coast, east Coast and north estuary), time (fixed, two levels, February/March (T1) and October/November (T2)) and site (random, two levels nested within combinations of habitat x time). Data were transformed to fix the left skewed distribution (as required based on λ values of Box–Cox plots) before calculating a matrix based on Euclidean distance. Post-hoc pairwise comparisons were used to explore significant factor effects using 9999 permutations. Each univariate trait of *H. banksii* was transformed as necessary (as required based on λ values of Box–Cox plots) and analysed with 3-factor ANOVAs with two fixed factors (habitat and time) crossed and one random factor (site) nested within the habitat x time interaction. Tukey's post hoc tests were conducted where we found significant effects. Differences in *H. banksii* morphology, based on five morphological traits (thallus length, mean number of branches, vesicle number, length and width) among habitat (N-coast v. E-coast v. N-estuary) at different times (February-March (T1) v. October-November(T2)) were displayed using a canonical analysis of principal coordinates (CAP) based on Euclidean distance.

Gastropod abundance and shell morphology

The spatial and temporal patterns in the abundance and shell morphology of *L. undulata* and *C. odontis* within each quadrat was analysed with ANOVAs, but because the two species did not occur in all habitats, we used different analyses for each species.

For *L. undulata*, we determined differences in the abundance between site, region and time with a three-way nested ANOVA. The factors were region (fixed, two levels, north v. east), time (fixed, two levels, February/March (T1) v. October/November (T2)) and site (random, two levels nested within each region x time interaction). No *L. undulata* occurred in estuaries so we only included coastal sites in these analyses. Data were transformed as

required based on λ values of Box–Cox plots prior to analyses. For *C. odontis*, we determined differences in the abundance among habitats at different times with a three-way nested ANOVA. The main factors were: habitat (fixed, three levels, N-coast v. E-coast v. N-estuary), time (fixed, two levels, February/March (T1) v. October/November (T2)) and site (random, two levels, nested within each habitat x time interaction).

To quantify the differences in shell morphology between site, region, habitat and time we measured five morphological traits on the shells of 40 individuals of both species using Vernier callipers (Craftright, 0.01 mm resolution). These were: shell length, shell width, full and inner aperture and shell thickness. The first two measures represented the overall size of the individual, while the outer and inner aperture indicated the maximum spread of the foot on the substrate. Shell thickness was measured at the point of maximum breakage on the outer lip of the shell, to evaluate the risk of shell-breaking predation and exposure at each site.

Differences in the shell morphology of both species were determined using permutational analyses of variance (PERMANOVA). Traits were transformed as required based on λ values of Box–Cox plots before calculating a matrix based on Bray-Curtis distance. For *L. undulata*, we used a three factor permutational multivariate analysis of variance (PERMANOVA) with the main factors region (fixed, two levels), time (fixed, two levels) and site (random, two levels) nested with the region x time combination. In addition, each shell trait was analysed with three-factor ANOVAs, with two fixed factors (region and time) crossed and one random factor (site) nested within the region x time interaction. Because we were unable to collect enough *C. odontis* at time two (T2), we used a two-way PERMANOVA with the main factor habitat (3 fixed levels) and site (random, two levels) nested within each habitat level. Post-hoc pairwise comparisons were used to explore significant factor effects using 9999 permutations. Each shell trait was analysed with two-

factor ANOVAs, with one fixed factor (habitat) and one random factor (site) nested within each habitat. Principal Component Analysis (PCA) was used to visualise differences in the shell morphology between regions (north v. east) and time (February/March v. October/November) for *L. undulata* and among habitats (N-coast v. E-coast v. N-estuary) for *C. odontis*.

Relationships between H. banksii morphology and gastropod morphology

Initially, the data were visualized using Draftsman plots to check for correlations between variables and detect any skewed distributions requiring transformation. For *H. banksii* morphology all variables were transformed (as required based on λ values of Box–Cox plots) to fix the mildly left-skewed distribution. For shell traits of *L. undulata* and *C. odontis,* data were also transformed (as required based on λ values of Box–Cox plots) to fix the mildly left skewed distribution. For both species, shell length and diameter and full and inner aperture were highly correlated ($r > 0.9$) and thus shell diameter and inner aperture were deleted before calculating matrices matrix based on Bray-Curtis distance. We then determined the relationship between *H. banksii* morphology and shell traits for each gastropod species separately using two different multivariate approaches. First, the BIOENV procedure from the PRIMER software package (ver. 6, K. R. Clarke and R. N. Gorley, PRIMER-E, Plymouth, UK) was used to identify which *H. banksii* traits were correlated with the gastropod shell morphology based on Euclidean distance. Second, a distance based linear model (DISTLM), with stepwise regression as selection criteria, was used to find the most parsimonious model of *H. banksii* variables predicting the patterns of gastropod morphology (Anderson et al. 2008). The Akaike criterion model (An Information Criterion, Akaike 1973) was used as selection criteria and a smaller AIC value indicated the best combination of predictor variables (Anderson et al., 2008). The dbRDA routine performed a constrained ordination of the reduced gastropod morphological data using the most parsimonious model

identified by DISTLM to explain the variation in the gastropod morphology with a smaller set of predictor variables used to identify which *H. banksii* morphological traits affected the gastropods shell size most.

Results

***H. banksii* morphology**

There was significant variation of *H. banksii* morphology across habitats and time, as well as among sites (PERMANOVA, Table 3.1).

Table 3.1: Results of PERMANOVA to test the effects of Habitat, Time and Site on the morphology of *Hormosira banksii*. The analysis was based on Euclidean distances on box-cox transformed data following 9999 permutations of residuals under the full model. Abbreviations: Ha = habitat; Ti = time; Si = site; Res = Residuals; Ha x Ti(Si), the site is nested within the main factors; R^2, percentage contribution of each factor to the overall of variation; MS, mean square. Abbreviations for pairwise comparison: N-coast = north coast, N-estuary = north estuary, E-coast = east coast.

	Df	MS	F	R^2	Pr(>F)	pairwise comparisons
Ha	2	0.204	87.37	48.7	< 0.0001	N-coast ≠ N-estuary ≠ E-coast
Ti	1	0.013	5.60	1.6	< 0.001	
Ha x Ti	2	0.003	1.63	0.9	0.15	
Ha x Ti(Si)	6	0.016	7.22	12	< 0.0001	
Res	132	0.002		36.8		
Tot	143			1		

Differences among habitat accounted for the greatest amount of the overall variation (49%) and pairwise comparisons indicated large differences between the north coast and the other two habitats at both times although the east coast and north estuary were still significantly different (Table 3.1, Fig. 3.2). Differences among sites within habitat accounted for 12% of the variation (Table 3.1).

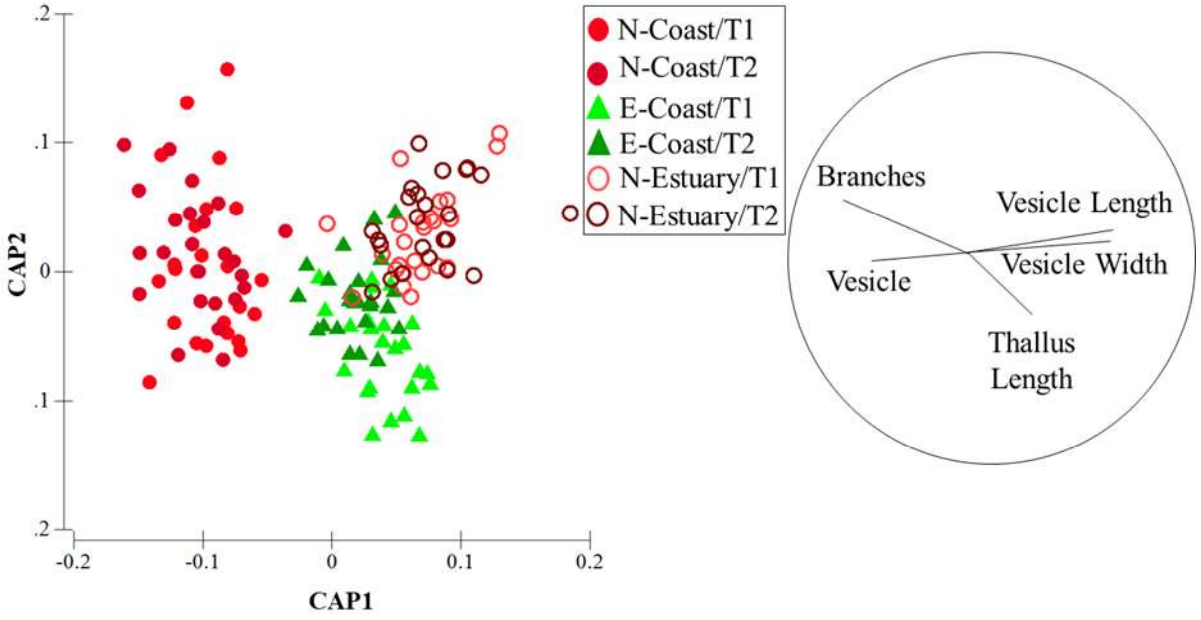

Figure 3.2. Canonical analysis of principal coordinates (CAP) of five morphological traits of *Hormosira banksii* across habitats (coast and estuary) and regions (east and north), at two times (February–March (T1) and October–November (T2)) pooled across sites for each habitat, region and time. N-Coast/T1, north coast in February–March; N-Coast/T2, north coast in October–November; E-Coast/T1, east coast in February–March; E-Coast/T2, east coast in October–November; N-Estuary/T1, north estuary in February–March; N-Estuary/T2, north estuary in October–November. Twelve thalli were sampled for each habitat, region and time. Inset shows the vectors based on Pearson correlation for the morphological traits.

The CAP revealed a clear separation between the three habitat along CAP1 (Fig.3.2), with vectors reflecting the presence of individuals with a highly branched structure and many, small vesicles in the north, which increase in length and width on the east coast and were largest in the estuary where *H. banksii* had large spherical vesicles, 2-3 times the size as those on the north coast (Table 3.2).

Table 3.2: Mean (±SE) values of the morphological traits of *Hormosira banksii* for sites in two habitats (Coast and Estuary), regions (North and East), times (February/March and October/November) and six sites (four on the coast and two on the estuary)**.** Site abbreviations as in Fig. 3.1.

Site	Habitat/ Region	Time	Thallus Length	Branch Number	Vesicle Number	Vesicle Length	Vesicle Width
NC1	N-Coast	Feb/Mar	18±1.4	113±32.04	702±113.03	0.52±0.02	0.44±0.01
NC2	N-Coast	Feb/Mar	17±1.4	360±83.7	1329±225.1	0.48±0.01	0.37±0.02
EC1	E-Coast	Feb/Mar	18±1.3	38±7.25	312±59.9	1.72±0.04	1.33±0.03
EC2	E-Coast	Feb/Mar	18±1.2	41±8.9	208±46.3	1.14±0.06	0.65±0.03
NEs1	N-Estuary	Feb/Mar	28±2.6	72±16	256±57	1.41±0.07	0.85±0.05
NEs2	N-Estuary	Feb/Mar	25±1.9	148±25.3	450±101	1.68±0.06	1.25±0.05
NC1	N-Coast	Oct/Nov	15.28±1.1	76±8.4	423±66.9	0.5±0.02	0.4±0.01
NC2	N-Coast	Oct/Nov	14.6±1.5	346±86.4	1071±262.8	0.4±0.01	0.3±0.01
EC1	E-Coast	Oct/Nov	20±1.3	23±3.9	133±24.7	1.1±0.03	0.7±0.02
EC2	E-Coast	Oct/Nov	21.91±1.9	55±7.1	271±50.1	1±0.04	0.5±0.03
NEs1	N-Estuary	Oct/Nov	28.14±2.7	84±16.2	213±33.4	1.5±0.08	0.9±0.04
NEs2	N-Estuary	Oct/Nov	31.45±2.7	89±10.1	293±41	1.5±0.07	1±0.04

Univariate analysis showed significant 3-way interactions between site, habitat and time for vesicle length and width and number of branches (all $P < 0.0001$), as well for vesicle number ($P < 0.001$). In contrast thallus length, differed slightly between habitat and site (ANOVA, $F = 3.33$, $p < 0.01$), reaching the biggest size in the estuary.

Gastropod abundance and shell morphology

Differences among habitats in the abundance and shell size of gastropods varied among habitat at different times, depending on the species identity. *Lunella undulata* only occurred on the coast, and its abundance differed significantly between regions dependent on sampling (Table 3.3, Fig. 3.3), with the highest abundance of snails found at one site on the east coast (EC1), but only in February/March (T1, Tukey's test, $P < 0.0001$).

Table 3.3: ANOVA testing the effects of Region, Time and Site on the abundance of *Lunella undulata* (A). Abbreviations: Re = Region, Ti = Time, Si = Site, Re or Ha x Ti(Si), the site is nested within the main factors Res = Residuals, Nc = north coast, Ec = east coast, T1 = time 1, T2 = time 2.

	Df	MS	F	Pr(>F)	pairwise comparisons
Re	1	1.89	39.97	< 0.001	
Ti	1	0.01	0.35	0.551	
Re x Ti	1	0.32	6.85	0.009	Ec/T1 > Ec/T2 > Nc/T2 > Nc/T1
Re x Ti(Si)	8	1.10	23.3	< 0.0001	
Res	132	0.04			

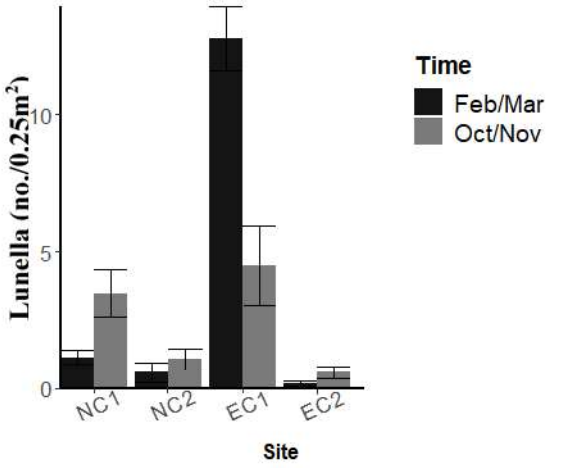

Figure 3.3. Mean (± SE) abundance of *Lunella undulata* per quadrat in two habitats (north coast and e ast coast), at two times (February/March and October/November) and two sites (NC1 = Bell Buoy Be ach, NC2 = Greens Beach, EC1 = Falmouth, EC2 = Shelly Beach) within each habitat. Each column r epresents n =12 replicates.

Shell morphology of *L. undulata* also varied significantly between region and time, as well as between site within each region x time interaction, which explained just a small part of the overall variation (25%, PERMANOVA Table 3.4). Differences between region and time accounted for another 4.8% of the total variation and pairwise comparisons showed significant differences between all possible combinations of coast and time (Table 3.4 A, Fig. 3.4).

Table 3.4. PERMANOVA testing the effects of Region, Time and Site on the morphology of *Lunella undulata*. Analyses were based on Bray–Curtis distances on transformed data following 9999 permutations of residuals under the full model. Abbreviations: Re, = region; Ti = time; Si = site; Res = Residuals; Re x Ti(Si), is the site is nested within the main factors Ha = habitat; Ha/Si is Site nested within each Habitat; R^2, percentage contribution of each factor to the components of variation; MS, mean square. Abbreviations for pairwise comparison: NC/T1 = North coast in February/March, NC/T2 = North coast in October/November, EC/T1 = East coast in February/March, EC/T2 = East coast in October/November, NE = North estuary, EC = East coast, NC = North coast.

	Df	MS	F	R^2	Pr(>F)	pairwise comparisons
Re	1	0.0001	8.79	1.6	< 0.0001	
Ti	1	0.0009	51.05	9.6	< 0.0001	
Re x Ti	1	0.0004	25.44	4.8	< 0.0001	NC-T1 ≠ NC-T2 ≠ EC-T1 ≠ EC-T2
Re x Ti(Si)	4	0.0006	32.71	25	< 0.0001	
Res	312	0.0000		59		
Tot	319			1		

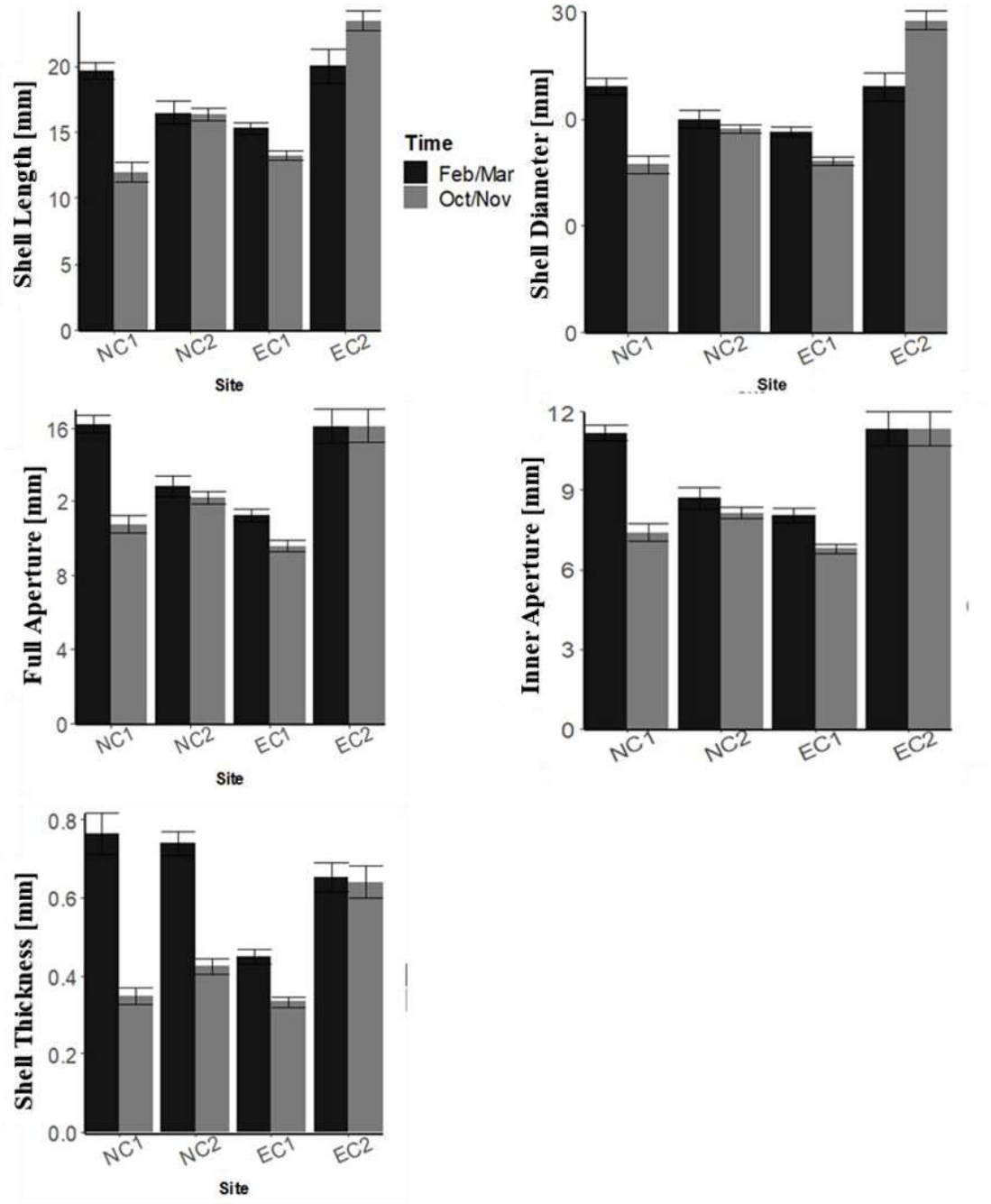

Figure 3.4. Mean (± SE) values of five *Lunella undulata* morphological traits sampled in two Regions (North and East) and two sites within each region at two times (February/March and October/November). Each column represents n= 40 replicates. Abbreviations: NC1 = Bell Buoy Beach, NC2 = Greens Beach, EC1 = Falmouth, EC2 = Shelly Beach.

The PCA (Fig. 3.5) also highlighted a temporal separation between regions at different times, with vectors for shell length and aperture indicating an overall decrease in the shell size at time 2 just on the north coast. Instead on the east coast, particularly at EC2, vectors for shell traits indicated the presence of the biggest shells with large apertures and the thickest shells at

time 2. Univariate analysis showed significant 2-way interactions between site, region and time for all the shell traits ($P < 0.0001$).

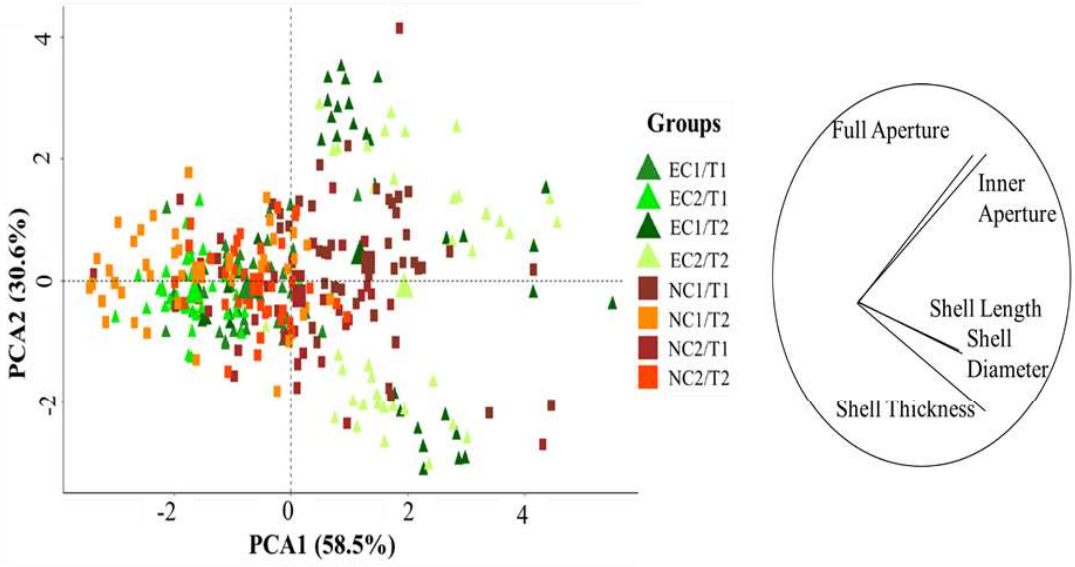

Figure 3.5. Principal Component Analysis (PCA) of five morphological traits of *Lunella undulata* between two regions (north and east), at two times (February/March and October/November) and two sites within each region. Abbreviations: NC1/T1: Bell Buoy Beach in February–March, NC1/T2: Bell Buoy Beach in October–November, NC2/T1: Greens Beach in February–March, NC2/T2: Greens Beach in October–November, EC1/T1: Falmouth in February–March, EC1/T2: Falmouth in October–November, EC2/T1: Shelly Beach in February–March, EC2/T2: Shelly Beach in October–November. Forty individuals of each species were sampled for each site, region and time.

Chlorodiloma odontis had a broader distribution than *L. undulata*, occurring on both coasts and in the north estuary. Significant differences in the abundance occurred between habitat and time (Table 3.5) and post-hoc tests indicated the north coast had significantly higher abundance than the north estuary and then the east coast having the lowest (Table 3.5, Fig.3.5). *C. odontis* shell morphology also varied significantly at all spatial scales (PERMANOVA Table 3.6).

Table 3.5. ANOVAs testing the effects of Habitat and Site on the abundance of *Chlorodiloma odontis*. Abbreviations: Ha = Habitat, Re = Region, Ti = Time, Si = Site, Re or Ha x Ti(Si), the site is nested within the main factors Res = Residuals, N-coast = north coast, N-estuary = north estuary, E-coast = east coast.

	Df	MS	F	Pr(>F)	post-hoc
Ha	2	1.88	87.25	< 0.001	
Ti	1	0.55	25.73	< 0.001	
Ha x Ti	2	0.12	5.94	0.003	Nc/T2 > Nc/T1 > Nest/T1> Nest/T2> Ec/T2 > Ec/T1
Ha x Ti(Si)	6	0.10	5.07	< 0.001	
Res	132	0.02			

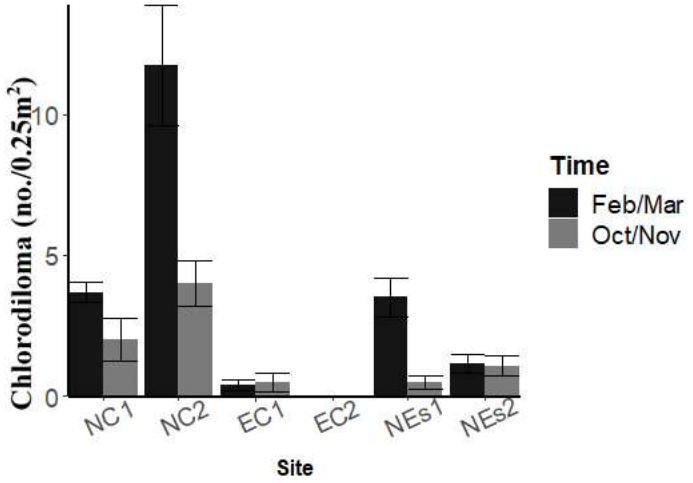

Figure 3.6. Mean (± SE) abundance of *Chlorodiloma odontis* per quadrat in three habitats (N-Coast, E-Coast and N-Estuary) and two sites within each habitat. Each column represents n =12 replicates. Abbreviations: NC1 = Bell Buoy Beach, NC2 = Greens Beach, EC1 = Falmouth, EC2 = Shelly Beach, Nest1 = Clarence Point, Nest2 = George Town.

Table 3.6. PERMANOVA testing the effects of Habitat and Site on the morphology of *Chlorodiloma odontis* during February/March. Analyses were based on Bray–Curtis distances on transformed data following 9999 permutations of residuals under the full model. Abbreviations: Ha = habitat; Ha(Si) is the site is nested within the main factors, R2, percentage contribution of each factor to the components of variation; MS, mean square. Abbreviations for pairwise comparison: NC = North coast, EC = East coast, NE = North estuary.

	Df	MS	F	R^2	Pr(>F)	pairwise comparisons
Ha	2	0.536	131.76	45.2	< 0.0001	EC ≠ NC ≠ NE
Ha(Si)	3	0.115	28.34	14.6	< 0.0001	
Res	234	0.004		40.2		
Tot	239			1		

Differences among the three habitats accounted for a greater part of the total variation (45.2%) than differences between site and habitat (14.6%) and pairwise comparisons showed significant differences between the N-coast and E-coast (p-value = 0.001) and between the N-estuary and E-coast (p-value = 0.001) and between the NC and Nest. In the PCA (Fig. 3.7) vectors for shell length and diameter clearly showed the separation of the N-estuary from other habitats, where shells were smallest. Vectors for shell aperture and thickness showed the presence of shells with the largest apertures on the E-coast and the thickest ones on the N-coast (Fig. 3.7, 3.8).

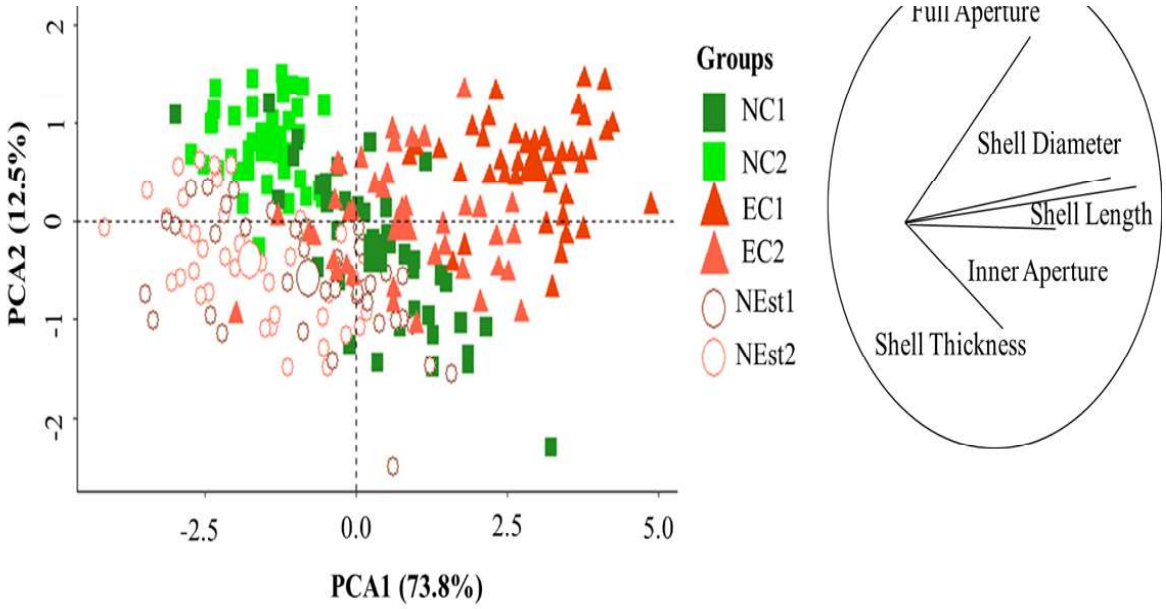

Figure 3.7. Principal Component Analysis (PCA) of five morphological traits of *Chlorodiloma odontis* across three habitats (N-Coast, E-Coast and N-Estuary) and two sites within each habitat. Abbreviations: NC1 = Bell Buoy Beach in February–March, NC2 = Greens Beach in October–November, EC1= Falmouth in February–March, EC2 = Shelly Beach in October–November, Nest1 = Clarence Point in February–March, Nest2 = George Town in October–November. Insets show the vectors based on Pearson correlation for the morphological traits. Forty individuals of each species were sampled for each site and habitat in February/March.

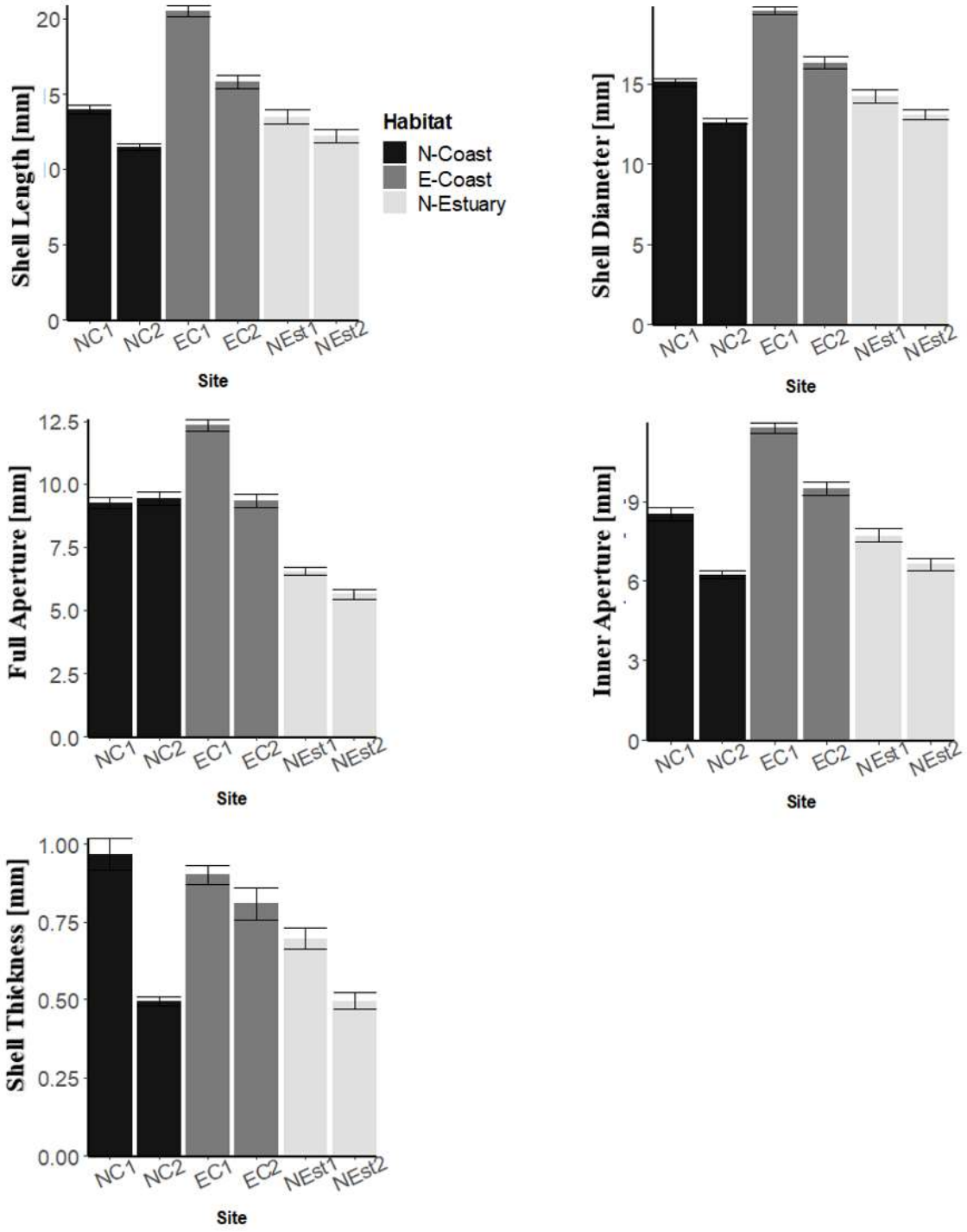

Figure 3.8. Mean (± SE.) values of five *Chlorodiloma odontis* morphological traits sampled in three habitats (N-Coast, E-Coast and N-Estuary) and six sites (two for each habitat). Each column represents n=40 replicates. Abbreviations: N-Coast/T1 = North coast February/March, N-Coast/T2 = North coast October/November, E-Coast/T1 = East coast February/March, E-Coast/T2 = East Coast October/November.

Relationships between H. banksii morphology and gastropod morphology

Overall these analyses suggested that thallus length and vesicles size of *H. banksii* correlated with gastropod shell morphology, but the contribution of these traits on gastropods shell traits varied between the two species.

The BIOENV procedure performed on a resemblance matrix based on Bray-Curtis distance, identified vesicle length and width of *H. banksii* as the best pair of variables correlated with *L. undulata* shell morphology, although the overall correlation was low (r = 0.098). The most parsimonious model from the DISTLM procedure only selected thallus length in the marginal test, while in the conditional test vesicle length was significant, explaining 14% of the total variation (Table 3.7).

Table 3.7. DISTLM models for *Lunella undulata*. Marginal tests show the relative contribution of each variable tested individually. Conditional tests show best results for each number of variables fit into the model based on the Akaike information criterion (AIC). Prop., proportion of explained variation for each variable; SS, sum of squares; R^2, amount of variation explained. Variable abbreviations: V. Length = Vesicle length, V. Width = Vesicle width, M. Branch = mean number of branches.

Marginal Test

Variable	SS(trace)	Pseudo-F	P
1. Thallus length	747.63	3.24	0.06

Conditional Test (R^2 = 0.20, AIC = 507.66)

Variable	AIC	SS (trace)	Pseudo-F	P	Prop.
5. V. Width	522.93	731.98	3.252	0.06	0.03
4. V. Length	507.66	3254.8	16.93	0.0001	0.14

The dbRDA using the most parsimonious model identified by the DISTLM, showed a clear separation of shell morphologies between the E-coast and N-coast along dbRDA2 (Fig. 3.9). Along dbRDA1, differences in vesicle length and width across times on the E-coast, aligned with the stronger variation of *L. undulata* shell morphology between eastern sites. Despite the contribution of *H. banksii* traits to the overall variation being low (20.3%), these

patterns highlighted a possible relationship between length and width of *H. banksii* vesicles and shell size of *L. undulata* on the east coast.

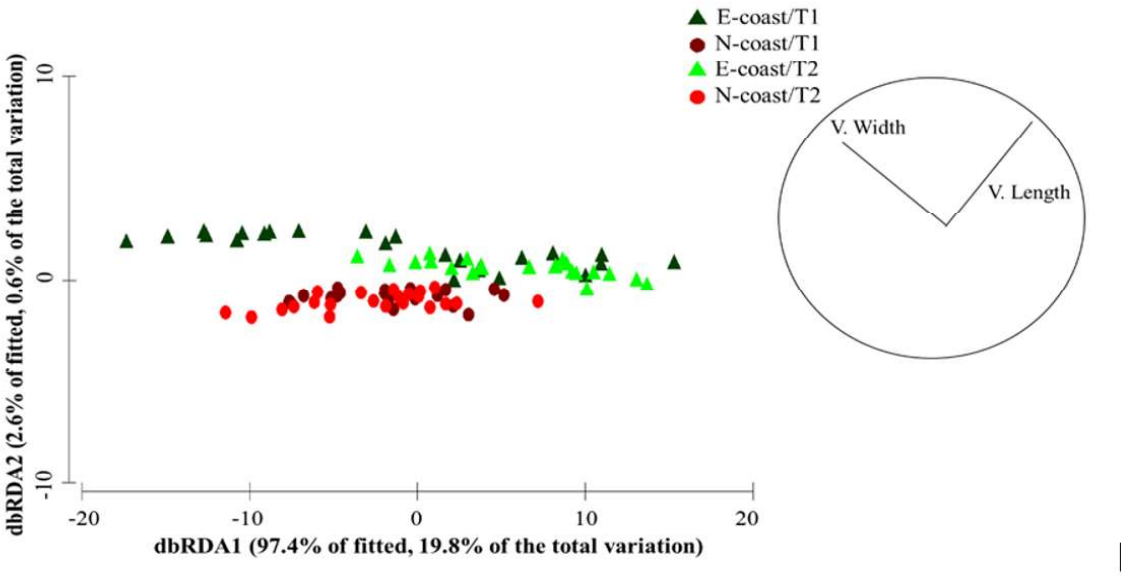

Figure 3.9. Distance-based redundancy analysis (dbRDA) ordination for the relationship between *Hormosira banksii* thallus morphology and *Lunella undulata* shell morphology pooled across sites within two regions at two times (n = 24, 50 x 50 cm quadrats for each region each time). N-Coast/T1 = north coast in February/March; E-Coast/T1 = east coast in February/March; N-Coast/T2 = north coast in October/November; E-Coast/T2 = east coast in October/November.

BIOENV also indicated a weak correlation between *C. odontis* shell morphology and thallus length, mean number of branches and vesicle width (r = 0.118). The most parsimonious model from the DiSTLM model selected two of the three variables identified by the BIOENV in the marginal test (thallus length and mean number of branches), but in the conditional test selected thallus length and vesicle width. Among these, thallus length contributed most (13%) to the total variation (Table 3.8).

Table 3.8. DISTLM model *Chlorodiloma odontis*. Marginal tests show the relative contribution of each variable tested individually. Conditional tests show best results for each number of variables fit into the model based on the Akaike information criterion (AIC). Prop., proportion of explained variation for each variable; SS, sum of squares; R^2, amount of variation explained. Variable abbreviations: V. Length = Vesicle length, V. Width = Vesicle width, M. Branch = mean number of branches.

Marginal Test

Variable	SS(trace)	Pseudo-F	P
1. Thallus length	447.28	10.71	0.0003
2. M. Branch	297.06	6.76	0.005

Conditional Test (R^2 = 0.18, AIC = 267.91)

Variable	AIC	SS (trace)	Pseudo-F	P	Prop.
1. Thallus length	270.66	447.28	10.71	0.0005	0.13
5. V. Width	267.91	186.52	4.70	0.02	0.05

In the dbRDA, using the most parsimonious model identified by the DISTLM, there was a small separation between N-estuary and N-coast along dbRDA2 reflecting the different shell morphology (smaller aperture and thinner shells) associated with wider vesicles in estuaries. Along dbRDA2, the separation between the N-estuary and E-coast groups highlighted an association with thallus length (- 0.9) which reflected the long thalli and the generally smaller morphology for most traits for *C. odontis* in the N-estuary (Fig. 3.10) compared to the E-coast. Although the overall variation in *C. odontis* morphology explained by *H. banksii* traits was low (R^2 = 18%, AIC = 267.91), these patterns highlighted, as for *L. undulata*, an association between *H. banksii* traits and *C. odontis* morphology depending on habitat and suggests a possible relationship between smaller shells and the larger *H. banksii* thalli in the estuary.

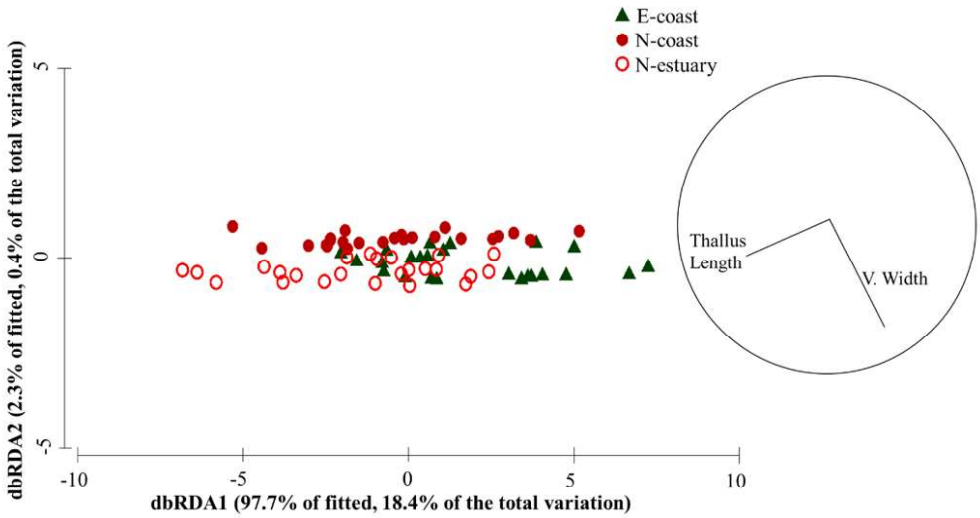

Figure 3.10. Distance-based redundancy analysis (dbRDA) ordination for the relationship between *Hormosira banksii* morphology and *Chlorodiloma odontis* morphology pooled across sites within three habitats (N-coast, E-coast and N-estuary) (n = 12, 50 x 50 cm quadrats for each habitat). The inset shows the vectors based on Pearson correlation for *Hormosira* morphological traits that contribute most towards explaining overall and fitted variation with the dbRDA axes. N-Coast = north coast; E-Coast = east coast; N-Estuary = north estuary.

Discussion

This study shows that the abundance and morphology of two common gastropods associated with the habitat-forming alga *H. banksii* differs between regions, habitats and sites. While these regions and habitats have different morphs of *H. banksii* they also have different environmental conditions including tidal regimes and wave exposure. Nonetheless, although gastropod morphology was variable within species, there were some indications of an association between gastropod morphology and *H. banksii* morphology. For *L. undulata* which generally occurred on the substratum beneath the *H. banksii* canopy, or in crevices, there was an association between shell morphology (generally larger shell traits) and larger *H. banksii* vesicles on the more exposed east coast compared to the north coast. In contrast,

for *C. odontis*, which is typically found attached to the thallus, there was an association between a smaller morph (particularly a smaller outer aperture) and the longer *H. banksii* morph with wider vesicles found in estuaries. Overall, these results suggest an influence of seaweed morphology but also an interactive effect with environmental factors (wave exposure and tidal range).

Lunella undulata occurs in low intertidal and shallow subtidal zones and is often abundant in wave-exposed environments (Edgar 1997; Shepherd, 2013; Grove 2017). The highest abundance of *L. undulata* occurred at EC1, which was the most wave-exposed site. In New South Wales (NSW), smaller *L. undulata* tend to occur in the canopies of *H. banksii* (Smoothey 2013) which has a similar morphology to *H. banksii* found on the east coast of Tasmania or, in coralline algal habitats (Worthington and Fairweather 1988) whereas larger *L. undulata* often occur in crevices and areas without seaweed. Similarly, at EC1, we observed small *L. undulata* within canopies at EC1 of *H. banksii* and larger individuals in the crevices at EC2. At EC1, *L. undulata* were often attached to *H. banksii* vesicles, which were relatively long and wide, and the relatively small apertures of these snails may have allowed strong attachment to the larger vesicles at this site. Small gastropods with relatively large apertures typically occur at wave-exposed sites (Boulding 1990; Trussel et al. 1993; Boulding et al. 1999), and the reduced foot size of *L. undulata* is clearly against of these findings. However, since *H. banksii* is likely to reduce wave energy, offering sheltered habitat with a reduced risk of dislodgement to *L. undulata*, even a reduced foot size may provide enough attachment strength to snails. Thus, the possible relationship between larger *H. banksii* vesicles at EC1 and larger shell size of *L. undulata* with a reduced foot size may indicate an influence of *H. banksii*, on the shell traits of *L. undulata* through the provision of protective environment. Although attachment strength may be important, juveniles may additionally recruit to *H. banksii* where they gain protection from predators or high temperatures

(Hayakawa et al. 2013) until they grow too large to live in the seaweed canopies (Hayakawa et al. 2008).

On the north coast shells *L. undulata* shells tended to be smaller but thicker in association with the smaller *H. banksii* vesicles although, most *L. undulata* occurred beneath canopies on this coast. Thick shells with small apertures can reduce predation and desiccation (Atkinson and Newbury 1984; Johannesson 1986). The semidiurnal tidal cycle at northern sites with two low tide of approximately equal length leaves organisms exposed to the air for more time and the small *H. banksii* may minimize heat and desiccation stress at low tide and, as well, allow *L. undulata* individuals to hide from shell-breaking predators (e.g. crabs).

In contrast to *L. undulata*, the highest abundance of *C. odontis* occurred on the north coast associated with the small, bushy *H. banksii* morph. Here, *C. odontis* was usually attached to *H. banksii* vesicles or within the branches. *Lunella undulata* was also common in the north estuary where the *H. banksii* reached its largest size (~30 cm of length and ~1 cm vesicles). The high abundance in association with the north coast morph suggests an influence of this thallus structure on its distribution. Seaweeds with a fine, more branched structure often support more gastropods than less branched species (Gee and Warwick 1994; Chemello and Milazzo 2002, Tuya 2008). However, *H. banksii* with large vesicles from estuaries also supported relatively high densities of *C. odontis*, similar to findings in NSW where gastropods were more abundant in estuaries than on rocky shores where *H. banksii* had smaller vesicles (Bishop et al. 2009). It appears that an association between *C. odontis* and *H. banksii* morphology may vary with location and the capacity of different morphs at different densities to modify environmental conditions (bioengineer potential). The extensive beds of *H. banksii* on the north coast of Tasmania provide a thick cover at low tide and can reduce temperature by up to 5°C beneath the canopy (Gemelli et al. in preparation). This may provide favourable microhabitats (reduced abiotic stress and predation pressure) for species

that use the canopy as habitat (Wright et al. 2014). The presence of the typically coastal *C. odontis* on *H. banksii* in the N-estuary of the Tamar River likely reflects the large seawater inflow into this estuary from Bass Strait, which maintains the salinity range between 33PSU and 35PSU (Edgar and Barrett 1999). More broadly, differences in the abundance of both *L. undulata* and *C. odontis* between different regions and habitats are likely to influenced by a range of physical and biological factors as well as the capacity of each *H. banksii* morph to buffer environmental conditions at each habitat.

Similar to *L. undulata*, the generally larger shell size of *C. odontis* on the east coast may be related to stronger wave energy and the shells with large apertures at EC1 may reduce the risk of dislodgement by waves. Accordingly, *C. odontis* differently from other sites, was found more on rocks than *H. banksii* canopies at EC1 and thus exposed to strong drag forces which may explain the large foot size of *C. odontis* at this site. The smaller *C. odontis* on the north coast associated with the small *H. banksii* morph may be due to weaker wave energy and a possible relationship between vesicle width and shell size of this species. On the north coast, *C. odontis* was often observed with their foot wrapped around a chain of vesicles or branches (F. Gemelli personal observations) which may allow snails to avoid dislodgement despite the small vesicle size. The reduced shell length of *C. odontis* in the north estuary compared to the other two habitats, is in contrast to previously reported patterns of large and thick shells in gastropods that occur on wave-sheltered shores (Boulding 1990; Boulding and Van Alstyne 1993; Trussel et al. 1993). As for *L. undulata*, large and thick shells in the north may represent a defence against shell breaking predators (e.g. crabs) and possibly fishes, which have difficulties in handle and eat large and thick shells in their mouthparts (Ivlev 1961; Vermeij 1974; Palmer 1979; Bertness and Cunningham 1981; Johannesson 1986) or reduce desiccation and temperature stress (Jones and Boulding 1999). However, this further indicates a relationship between thallus length and shell size of *C. odontis*: long thalli and

large vesicles in the N-estuary may provide a good surface for attachment and additional protection against desiccation at low tide.

Overall, despite the marginal influence of *H. banksii* morphological traits on gastropod abundance and shell morphology, our results suggest species-specific responses to different *H. banksii* morphs. Each *H. banksii* morph may engineer different microhabitats due to the different thallus architecture, affecting abundance and shell morphology. However, since the biogeographic context in which species occur is determined by dispersal, disturbance-colonization dynamics at large scales and, by microhabitats at smaller scales, manipulative experiments will help tease apart the effect of *H. banksii* morphology, depending on local environmental conditions on gastropod morphology.

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4 Chapter: Different densities and morphologies of an intertidal ecosystem engineering seaweed affect gastropod abundance

Federica Gemelli, Craig R. Johnson, Jeffrey T. Wright

Abstract

Canopy-forming seaweeds are important bioengineers and foundation species in the intertidal zone, providing habitat and attenuating the physical conditions via the creation of canopies. The strength of abiotic modifications and the effects on associated species can depend on the characteristics of the engineer (morphology and density) as well as the baseline level of environmental stress. The fucoid *Hormosira banksii* dominates intertidal rocky shores in southeast Australia where it provides habitat for a range of invertebrate species. The morphology of this species is highly variable, with two distinct morphs growing respectively on the north (small morph) and east (standard morph) coasts of Tasmania. Here, through a series of manipulative field experiments we investigated how changes in the density and morphology of *H. banksii* affect its ability to alter temperature and light levels beneath the canopies and how these modifications influence the abundance of common gastropod species. Canopies reduced temperature by ~20% and light by ~90% but these metrics did not differ among different *H. banksii* density and morphs treatments. However, gastropod abundance was affected by these factors, with the greatest abundance occurring within dense canopies of *H. banksii*. Despite the evidence that gastropods species use *H. banksii* canopies as habitat, their abundance was not correlated with reductions in temperature and light. Nevertheless, our study is the first attempt to tease apart the factors determining the bioengineering potential of *H. banksii*.

Introduction

Canopy forming seaweed dominate temperate intertidal and subtidal rocky shores where they support biodiverse and productive ecosystems (Jenkins et al. 1999; Bulleri et al. 2001; Bennett and Wernberg 2014). In the intertidal zone, the daily rise and fall of tides exposes organisms to extremes in important environmental parameters including temperature, humidity, and light (Davison and Pearson 1996; Jurgens et al. 2018; Pocklington et al. 2018). As ecosystem engineers (Jones et al. 1994), intertidal canopy-forming seaweed often reduce these abiotic stressors, as well as provide a refuge from predation, for small invertebrates beneath the canopy (Bertness et al. 1999; Bulleri et al. 2012; Wright et al. 2014).

In certain systems, the presence of single ecosystem engineering species can define the entire structure of associated biotic communities (Bruno et al. 2003). The effects of these species on assemblages can be positive (Bertness et al. 2004; Crain and Bertness 2006) or negative (Leonard 1999; Choi 2003; Beerman et al. 2013) and can depend on the background level of environmental stress among sites (Viejo 1999; Wright et al. 2018). Moreover, seaweed density (Bertness et al. 1999; Hendriks et al. 2010; Umanzor et al. 2018), morphology (size and shape, Christie et al. 2007; Hansen et al. 2010) and architecture (branching pattern, Bertocci et al., 2010; Best et al. 2017) can all influence the community structure of associated invertebrates. Thus, investigations into how these factors influence the engineering of the abiotic environment and subsequent effects on the associated biotic communities are important in understanding the role of canopy-forming seaweed in maintaining biodiverse intertidal communities.

Most studies of seaweed morphology and architecture have focused on comparisons between species (Wernberg et al. 2011 Veiga et al. 2014), showing that different species differentially buffer environmental stress. Seaweed with certain morphologies and architecture (e.g. branching pattern) provide different habitats (living space) and conditions

beneath the canopy (Crowe et al. 2013), which in turn affects the abundance of associated species (Attrill et al. 2000; Parker et al. 2001; Bates and De Wreede 2007; Cacabelos et al. 2010; Torres et al., 2015). Coarsely branched, vesiculate and stipitate algae tend to support the greatest abundance of invertebrates, particularly molluscs, likely due to their greater surface area for habitat, ability to trap food particles (Chemello et al. 2002) and provide protection from abiotic stress (Watt and Scrosati, 2013; Coombes et al. 2013; Umanzor et al. 2017). For example, dense canopies of the vesiculate *Ascophyllum nodosum* limits heat stress in summer in temperate regions (Bertness et al. 1999) and cold stress in winter in polar and subpolar regions (Scrosati and Ellrich, 2018), both of which negatively impact intertidal species. Similarly, a high biomass of the highly branched *Cystophora retroflexa* reduced ambient temperature by up to 30 % (A. Siciliano unpublished data) compared to *Gracilaria chilensis* (~ 10%). Although, the bioengineering potential of canopy forming seaweed has been explored (Wright et al. 2014; Watt et al. 2013; Umanzor et al. 2017), few studies have examined whether variation in the density and morphology in a single species (Bishop et al. 2009; 2012; 2013) affects its capacity to buffer environmental conditions (e.g. temperature and light) and thus, influence the quality of the habitat beneath the canopies for associated species.

Hormosira banksii is the most abundant canopy forming seaweed on intertidal rocky shores in Australasia, colonizing large areas with thick canopies, which provide habitat to many invertebrate species (Povey and Keough 1991; Keough and Quinn 1998; Lilley and Schiel, 2006; Bishop et al. 2009;2012;2013; Gemelli et al. 2018). The morphology (thallus length, branching pattern, vesicle number and size) of *H. banksii* is highly variable, differing among coastal rocky shores and estuaries (Ralph et al. 1998; Macinnis et al. 2005; Mueller et al. 2015; Gemelli et al. 2018), with the large estuarine morph having a positive effect on the

abundance of gastropods, most likely due to increasing the amount of living space and providing a substratum for biofilm growth on which grazers feed (Bishop et al. 2012;2013).

In Tasmania, southern Australia a small, highly branched *H. banksii* morph with small vesicles is found on the north coast where there are semi-diurnal tides and low wave exposure, while a longer, less branched 'standard' morph with larger vesicles occurs on the east coast where there are diurnal tides and greater wave exposure (Mueller et al. 2015, Gemelli et al. 2018). On the north coast the small morph often forms extensive mats (Fig. 4.1) that cover the rock at low tide. The different morphologies support distinct gastropod communities on each coast and a different abundance of common species (Gemelli et al. 2018), but whether these differences are due to different seaweed morphologies and/or densities on the different coasts and subsequently, their ability to modify the physical conditions beneath the canopies or reflect differences in environmental conditions (e.g. tidal regime, temperature, wave action) at the different sites, is still unclear.

Here, using two manipulative experiments, we investigated how different densities and morphologies of *H. banksii* affected the engineering of abiotic conditions and associated gastropod abundance. We hypothesised that (1) greater *H. banksii* densities and (2) canopies of the small north coast *H. banksii* morph would more strongly ameliorate temperature and light and thus influence the quality of the habitat provided to invertebrates, resulting in a higher abundance of gastropods compared to the larger east coast morph. To test these hypotheses, in the first experiment, we manipulated the density of the small morph on the north coast, while in the second experiment, different morphs of *H. banksii* were transplanted to a common recipient site in northern Tasmania. Variation in temperature and light beneath the canopies were measured as factors affecting the levels of thermal stress to which mobile species were exposed and, therefore, the choice by gastropods of sheltered habitats beneath *H. banksii* canopies.

Material and Methods

Study site and organisms

The experiments were carried out on an intertidal rocky shore at Beechford (41°01'22" S, 146°56'39" E) in the north of Tasmania. Experiments were initially done in 2017 (March-May) but were repeated in 2018 (February-May) due to very low gastropod densities in 2017. We only present results for 2018. Beechford faces Bass Strait and is largely protected from swell by the Australian mainland, and mostly subject to a moderate wind-driven waves (Short 2006). Like other sites on the north coast, Beechford has a semi-diurnal tidal regime, which results in many intertidal species being exposed to air twice every 24 hours. The shore is characterised by the presence of boulders in the range of 100 – 2,000 cm^2 which in the lower intertidal zones (below ~ 0.5 MLLW) are typically covered by *Hormosira banksii* with coralline turf (mostly *Corallina officinalis*) occurring as an understory.

Hormosira banksii has a small discoid holdfast with one to several fronds (1st branches) arising from it, made up of elongated water filled vesicles linked by short solid connectives (Osborn 1948, Bergquist 1959; Clarke et al. 1981; Macinnis-Ng et al. 2005; Mueller et al. 2015). The Turbo *Lunella undulata* (Lightfoot, 1786) and the Trochid *Chlorodiloma odontis* (W. Wood, 1828) are the most abundant gastropods associated with *H. banksii* on these coasts with *L. undulata* typically found beneath the canopy on the rock while *C. odontis* is typically attached on the vesicles. Although both species occur on the north and east coasts, *C. odontis* is more abundant in association with the small morph on the north coast and *L. undulata* is very abundant in association with the standard morph at one site on the east coast (Gemelli et al. 2018).

Effects of H. banksii canopy density

To determine how canopy density of *H. banksii* affected ecosystem engineering of the abiotic environment and gastropod colonisation we manipulated natural canopies of the small morph

at Beechford on the north coast to three density treatments: a control (C, 100% cover), half (H, 50% canopy cover) and quarter (Q, 25% canopy cover). In summer 2018 (February-May), 24 plots of *H. banksii* (25 x 25 cm) were haphazardly selected along a 100 m transect (MLLW ~0.5 m), marked with cable ties and randomly assigned to one of the three treatments (N = 8 replicates). *Hormosira banksii* was then removed by hand to the required cover and the edges of quadrats cleared to avoid any edge effect. No zero density plots were established as these gastropods are only found attached to *H. banksii* or beneath the canopies. All gastropods present within the quadrats were removed at the beginning of the experiment and placed at least three metres from the plots.

Effect of H. banksii morphology

To determine how *H. banksii* morphology affected ecosystem engineering of the abiotic environment and gastropod abundance we compared transplanted east and north coast morphs at a single site on the north coast (Beechford). In austral summer/autumn (February-May) 2018 the following four treatments were set up: 1) individuals collected from the east coast (Shelly Beach 42°34'00.5" S, 147°53'17.5" E) reattached on the north coast ("transplant (Tp)"), 2) individuals collected from the north coast (Beechford) reattached at a different place at the same site ("translocation (Ts)"), 3) an unmanipulated treatment where *H. banksii* was left intact ("control (C)") and 4) a treatment that contained ropes and epoxy attached beneath an intact canopy but without any *H. banksii* attached to the rope ("procedural control (Pc)") to determine the effects of rope and epoxy on gastropods. In 2017, a handling control (individuals collected and reattached in exactly the same place they were removed from) showed no effect on any metrics, so we did not use that treatment in the 2018 experiment. Treatments were established in 25 x 25 cm quadrats placed haphazardly along the shore (MLLW ~0.5 m), each replicated eight times and separated from other

quadrats by at least four metres. Quadrats were identified with underwater epoxy (A-788 Splash Zone, Z-SPAR, US) and cable ties of different colours positioned in the corners.

For the transplantation, translocation and handling control treatments, *H. banksii* were carefully removed from the substratum with a butter knife to avoid breakage of the holdfast and kept in seawater for 24 h. The next day a single thallus was inserted between strands of a piece of polypropylene rope (2 cm diameter, 8-9 cm long) by untwisting the strands and placing the holdfast between them before tightening it again. The rope was then firmly attached to the substratum, previously scrubbed to remove sand and coralline turf, with underwater epoxy at each end of the rope (Fig. 4.1).

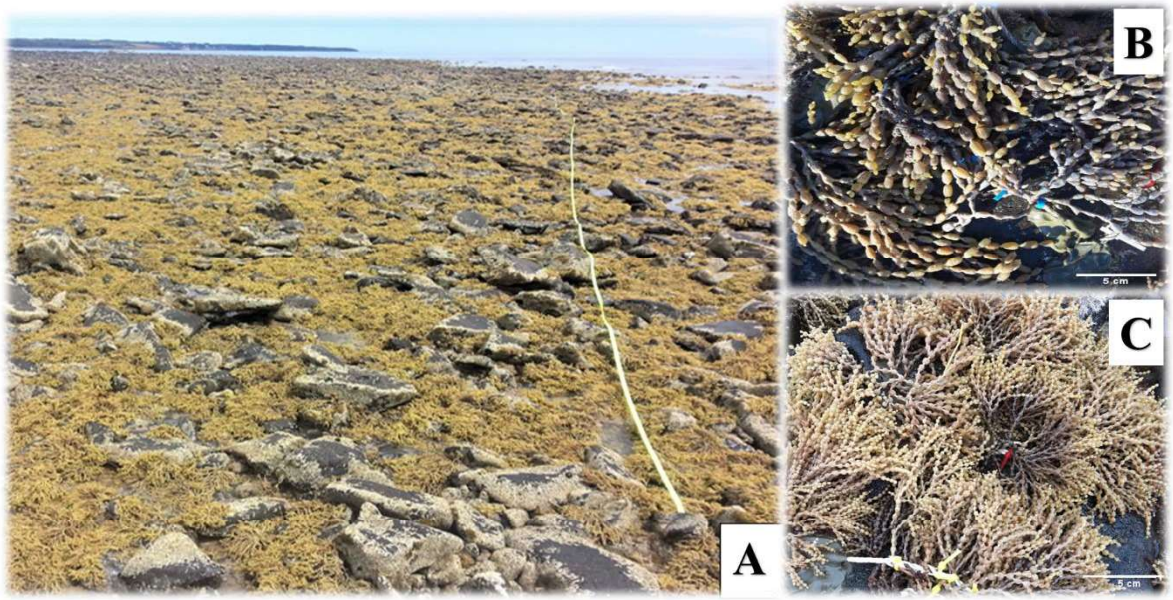


Figure 4.1. Photos showing A) the extensive canopies of the small morph of *Hormosira banksii* on the north coast of Tasmania (Beechford). The tape measure is 100 m in length. B) an experimental plot showing the transplanted standard morph, and C) an experimental plot showing the translocated small morph from the east coast.

These quadrats (except for the unmanipulated control) had the existing *H. banksii* and any gastropods removed by hand prior to attaching the experimental thalli. The cover of all treatments was standardised to 100% cover. The efficiency of this technique and the survival of *H. banksii* were tested in a pilot experiment between December 2016 and January 2017 in

three experimental quadrats for each morph. Both morphs survived well under these conditions after one month (98 % survivorship).

Measurement of temperature, light and gastropod abundance

Abiotic variables and gastropod abundance were measured in each quadrat every month. Temperature was measured beneath the canopy using a HOBO 4-channel thermocouple with three probes placed at three random points in each quadrat with a fourth probe placed outside of the canopies to measure ambient temperature. Probes were left for 10 seconds to obtain a stable measure. The reduction in temperature beneath the canopy for each quadrat was determined by subtracting the average of the three below-canopy temperatures from the ambient temperature. Both the absolute and percentage reduction in temperature were calculated. Light was measured using a HOBO MX2202 temperature/light logger with the probe placed at three points inside and outside the canopies and left for 10 seconds at each point. The extent to which canopies attenuated the light intensity were determined by subtracting the average of the light readings beneath the canopy from the ambient light and both absolute and percentage reduction calculated. No temperature or light data was obtained for May due to malfunctioning equipment. Gastropod abundance was determined by carefully searching each quadrat (both beneath and within the *H. banksii* canopy) each time.

Statistical Analysis

We determined differences in ambient temperature and light, the absolute and percentage reduction in temperature and light beneath the canopy vs. above and the abundance of gastropods among the different density and morphological treatments. For the density experiment (transformed as required based on values of λ from Box-Cox plots) data were analysed with a 2-way repeated measures ANOVA with the factors: treatment (fixed, 3 levels, control (C), half canopy (H) and quarter of canopy (Q)) and month (fixed, 3 levels, February, March and April for temperature and light with May included for gastropod

abundance). When it was not possible to use repeated measures ANOVA due to a violation of the assumption of sphericity, we used a multivariate analysis of variance (MANOVA), which does not have those assumptions. Effect size and Tukey post-hoc tests were also used to identify the contribution and difference between factors.

For the morphology experiment (transformed as required based on values of λ from Box-Cox plots to check variance homogeneity) we used a type III factorial repeated measures ANOVA, with the factors Treatment (fixed, 4 levels, Transplant (Tp), Translocation (Ts), Control (C), and procedural control (PC)) and month (fixed, 3 levels, February, March and April for temperature and light and four levels (including May) for gastropod abundance). Effect sizes were calculated for each factor as the percentage of the ratio of the sum of squares for each group level to the total sum of squares. Tukey post-hoc tests used to determine significant differences between levels of each factor.

To test the extent of any relationships between biological and abiotic data in both experiments we used multivariate approaches (BIOENV and DiSTLM), using the PRIMER statistical software (ver. 6, K. R. Clarke and R. N. Gorley, PRIMER-E, Plymouth, UK). However, none of the environmental variables contributed significantly to the gastropod abundance so we have not presented results from those tests.

Results

Environmental modifications by the different seaweed morphologies and density

Overall ambient temperature during the experiments ranged from 22.9°C during February to 14.8°C during April while light ranged from 88.94 klux in February to 29.4 klux in April (Figs. 4.2- 4.3 A-B).

In both experiments, temperature did not differ significantly with treatment or over months, but light was significantly lower in April compared to other months and in March compared to February (Tables 4.1- 4.2 A-F).

In the density experiment, *H. banksii* in all treatments reduced temperature and light to similar levels observed in the morphology experiment (Figs. 4.2 A-B) and there was also no significant difference in temperature and light reduction among density treatments (Figs. 4.2 C-D) which add a small contribution to the overall variation (Tables 4.1 C-D). Absolute and percentage temperature reduction was highest in March, then April and then February (Table 4.1 C-E). Absolute light reduction was highest in February, then March and then April (Table 4.1 D) but the percentage reduction in irradiance was similar and consistently high across months (> 80%, Table 4.1 F, Fig. 4.2 F)

Tables 4.1 A-F. Two-factor ANOVAs testing the effects of three density treatments (C, H, Q) and months (February, March and April) on ambient temperature (A), ambient light (B), absolute reduction in temperature (C) percentage reduction in temperature (E) and percentage reduction in light (F). Two-factor multivariate analysis of variance (MANOVA) testing the effect of three density treatments (C, H, Q) and months (February, March and April) on absolute light variation (D). Analyses were based on transformed data (Box-Cox transformation). Abbreviations for Source: Treat = Treatment, Mnt = Month.

A

Source	df	F-value	Pr (F)	Effect (η^{2})
Treat	2	0.49	0.61	0.04
Mnt	2	0.29	0.74	0.03
Treat x Mnt	4	0.45	0.76	0.03

B

Source	df	F-value	Pr (F)	Effect (η^{2})	Post-hoc
Treat	2	3.19	0.06	0.24	
Mnt	2	9.47	0.0004	0.58	Feb > March > April
Treat x Mnt	4	0.45	0.76	0.06	

C

Source	df	F-value	Pr (F)	Effect (η^{2})	Post-hoc
Treat	2	0.62	0.54	0.05	
Mnt	2	11.44	< 0.0001	0.5	Mar > April > Feb
Treat x Mnt	4	1.54	0.2	0.16	

D

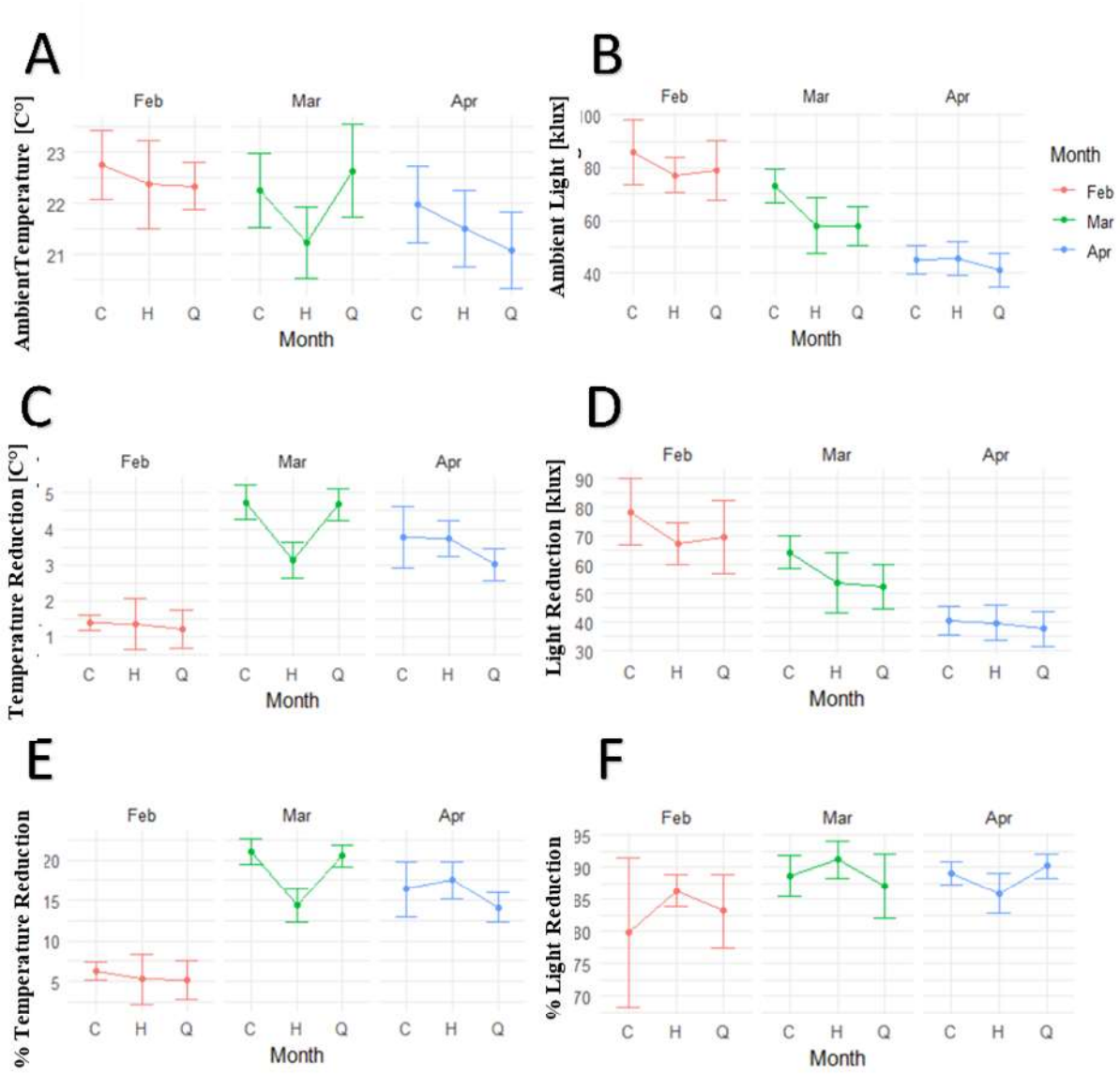
Source	df	Pillai	Approx F	N° Df	Den Df	Pr(>F)	Effect ($\eta^{\wedge 2}$)	Post-hoc
Treat	2	0.21	2.81	2	20	0.08	0.21	
Mnt	1	0.59	13.94	2	19	0.001	0.59	Feb > Apr > Mar
Treat x Mnt	2	0.14	0.78	4	40	0.53	0.07	

E

Source	df	F-value	Pr (F)	Effect ($\eta^{\wedge 2}$)	Post-hoc
Treat	2	0.59	0.56	0.05	
Mnt	2	12.44	< 0.0001	0.52	Mar > Apr > Feb
Treat x Mnt	4	1.45	0.23	0.16	

F

Source	df	F-value	Pr (F)	Effect ($\eta^{\wedge 2}$)	Post-hoc
Treat	2	0.74	0.48	0.06	
Mnt	2	0.15	0.85	0.01	Mar > Apr > Feb
Treat x Mnt	4	0.67	0.61	0.07	



Figures 4.2 A-F: Mean ± SE ambient temperature (A), ambient light (B), absolute reduction in temperature (C), absolute reduction in light (D), percentage reduction in temperature (E) and percentage reduction in light (F) among density treatments (Control (C), Half canopy (H) and Quarter of canopy (Q)) and months (February, March, April, May). Each line represents 8 replicates.

In the morphology experiment, *H. banksii* in all treatments reduced both temperature and light with absolut (and percentage) temperature reduced by up to 4.8°C (20%) and absolute (and percentage) light by up to 80 klux (90%). Temperature reduction (both absolute and percentage) beneath the canopy varied significantly among months but not among

morphology treatments (Tables 4.2 C, E; Figs. 4.3 C, E), with a contribution respectively of the 40% and 23% to the overall variation and the post-hoc tests showed temperature reduction was highest in March, then April, then February.

Similarly, absolute light reduction did not differ among morphology treatments (low contribution to the overall variation (Table 4.2 D), varying significantly only among months, which contributed most to the overall variation, with the highest reduction occurring in February, then March and then April (Table 4.2 D; Fig. 4.3 D). However, the percentage light reduction was consistently high (90%, Fig. 4.3 F) with no significant difference among treatments and months (Table 4.2 F).

Table 4.2 A-F. Two-factor ANOVAs testing the effects of four morphology treatments (C, PC, Ts, Tp) and three months (February, March, April and May) on ambient temperature (A), ambient light (B), absolute reduction in temperature (C), absolute reduction in light (D), percentage reduction in temperature (E) and percentage reduction in light (F). Analyses were based on transformed data (Box-Cox transformation). Abbreviations for Source: Treat = Treatment, Mnt = Month. Treat = Treatment, Mnt = Month.

A

Source	df	F-value	Pr (F)	Effect (η^2)
Treat	3	1.67	0.19	0.15
Mnt	2	0.22	0.79	0.01
Treat x Mnt	6	0.66	0.67	0.06

B

Source	df	F-value	Pr (F)	Effect (η^2)	Post-hoc
Treat	3	0.75	0.53	0.07	
Mnt	2	7.78	0.001	0.37	Feb > March > April
Treat x Mnt	6	0.56	0.75	0.05	

C

Source	df	F-value	Pr (F)	Effect (η^2)	Post-hoc
Treat	3	2.49	0.08	0.23	
Mnt	2	9.09	< 0.001	0.42	March > April > Feb
Treat x Mnt	6	1.66	0.14	0.16	

D

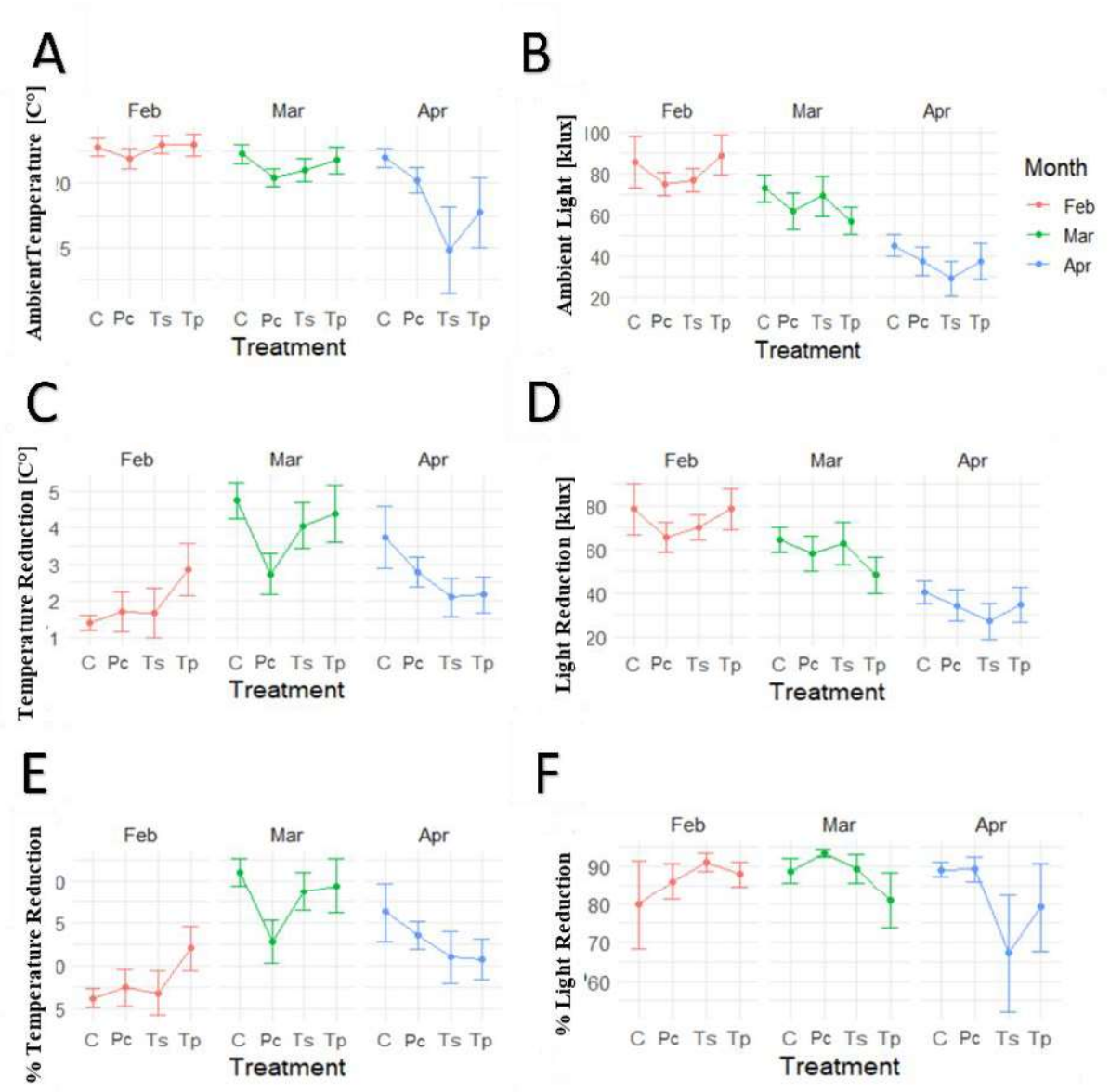
Source	df	F-value	Pr (F)	Effect (η^2)	Post-hoc
Treat	3	0.51	0.67	0.05	
Mnt	2	5.87	0.005	0.36	Feb > March > April
Treat x Mnt	6	0.43	0.85	0.04	

E

Source	df	F-value	Pr (F)	Effect (η^2)	Post-hoc
Treat	3	2.34	0.09	0.21	
Mnt	2	9.58	< 0.001	0.46	March > April > Feb
Treat x Mnt	6	1.46	0.2	0.15	

F

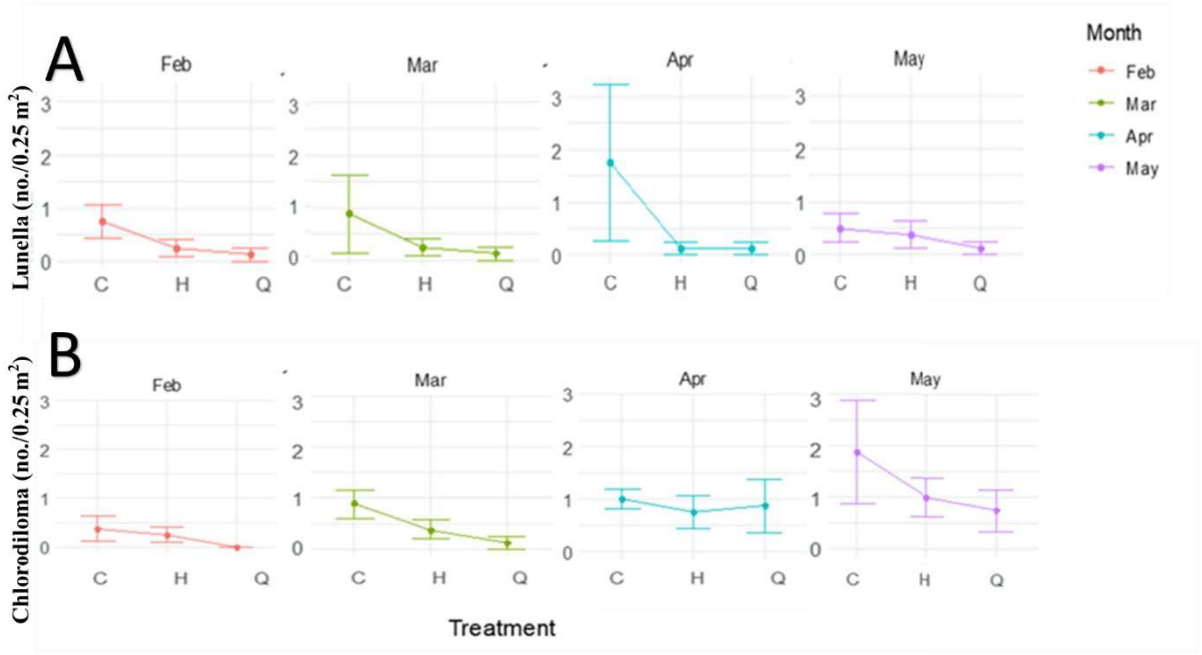
Source	df	F-value	Pr (F)	Effect (η^2)
Treat	3	0.79	0.5	0.08
Mnt	2	0.99	0.37	0.05
Treat x Mnt	6	0.69	0.65	0.08



Figures 4.3 A-F. Mean ± SE ambient temperature (A), ambient light (B), absolute reduction in temperature (C), absolute reduction in light (D), percentage reduction in temperature (E) and percentage reduction in light (F) among morphology treatments (Control (C), Procedural control (Pc), Translocation (Ts) and Transplant (Tp)) and months (February, March, April). Each line represents 8 replicates.

Effects of H. banksii morphology and density on the abundance of gastropods

In the density experiment the abundance of the two gastropod species was only slightly influenced by the different treatments, although generally, the full canopies hosted the greatest number of gastropods (Figs. 4.4 A-B).



Figures 4.4 A-B. Mean ± SE abundance of *L. undulata* (A) and *C. odontis* (B) among treatments (C, H, Q) and months (February, March, April, May). Each line represents 8 replicates.

Lunella undulata abundance was significantly higher in the control (100% cover) compared to the 25% cover treatment (Table 4.3 A, although this was marginally non-significant in the post-hoc test). The different density treatments contributed 27% of the variation in *L. undulata* abundance.

Tables 4.3 A-B. Two-factor ANOVA testing the effect of three density treatments (C, H, Q) and four months (February, March, April and May) on *L. undulata*. Analyses were based on transformed data (Box Cox transformation). Abbreviations for Source: Treat = Treatment, Mnt = Month. Two-factor ANOVA testing the effect of three density treatments (C, H, Q) and four months (February, March, April and May) on *C. odontis*. Analyses were based on transformed data (Box Cox transformation). Abbreviations for Source: Treat = Treatment, Mnt = Month.

A

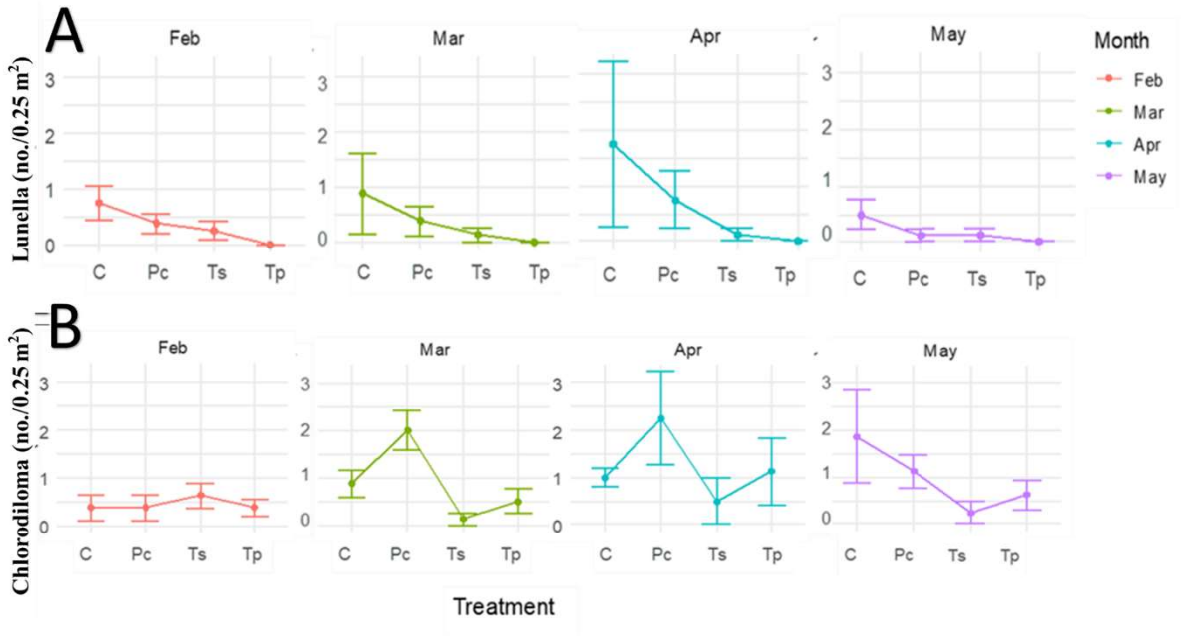
Source	df	Pillai	Approx F	N° Df	Den Df	Pr(>F)	Effect (η^2)	Post-hoc
Treat	2	0.17	2.26	2	21	0.12	0.17	
Mnt	1	0.27	2.38	3	19	0.1	0.27	
Treat x Mnt	2	0.11	0.4	6	40	0.86	0.05	

B

Source	df	Pillai	Approx F	N° Df	Den Df	Pr(>F)	Effect (η^2)	Post-hoc
Treat	3	0.27	3.95	2	21	0.03	0.27	C > Q
Mnt	1	0.11	0.79	3	19	0.51	0.11	
Treat x Mnt	2	0.1	0.35	6	40	0.9	0.05	

In contrast, *C. odontis* did not differ among canopy density treatments, although there were slightly more snails found in the 100% *H. banksii* cover treatment (33 snails) compared to the 50% (19 snails) and 25% (14 snails) cover treatments. *Chlorodiloma odontis* abundance did not differ among months (Table 4.3 B) despite the qualitative increase in the number of snails from February to May. Despite the lack of significant differences, time contributed slightly more (27%) than density treatments (17%) to the overall variation in *C. odontis* abundance (Table 4.3 B).

In the morphology experiment, the response of *L. undulata* and *C. odontis* to the different *H. banksii* morphologies differed among species (Figs. 4.5 A-B).



Figures 4.5 A-B. Mean ± SE abundance of *L. undulata* (A) and *C. odontis* (B) among treatments (C, Pc, Ts, Tp) and months (February, March, April, May). Each line represents 8 replicates.

Lunella undulata abundance varied among treatments but not month (Table 4.4 A) and post-hoc comparisons showed significant differences occurred between the control and the transplant from the east coast, which had no *L. undulata* at any time throughout the experiment, but not between any other treatments (Table 4.4 A, Fig. 4.5 A). Notably, the different morphology treatments contributed 29% of the variation in *L. undulata* abundance.

Tables 4.4 (A-B): Two-factor multivariate analysis of variance (MANOVA) testing the effect of four morphology treatments (C, PC, Ts, Tp) and months (February, March, April and May) on *L. undulata* (A). Two-factor multivariate analysis of variance (MANOVA) testing the effect of four morphology treatments (C, PC, Ts, Tp) and months (February, March, April and May) on *C. odontis*(B). Abbreviations for Source: Treat = Treatment, Mnt = Month.

A

Source	df	Pillai	Approx F	N° Df	Den Df	Pr(>F)	Effect (η^2)	Post-hoc
Treat	3	0.29	3.93	3	28	0.01	0.29	C > Tp
Mnt	1	0.11	1.11	3	26	0.36	0.11	
Treat x Mnt	3	0.1	0.33	9	84	0.96	0.03	

B

Source	df	F-value	Pr (F)	Effect (η^2)	Post-hoc
Treat	3	6.57	0.001	0.41	Pc > Ts, C > Ts
Mnt	3	1.77	0.15	0.15	
Treat x Mnt	9	1.68	0.1	0.14	

In contrast, *C. odontis* colonized all the experimental treatments and there was a significant treatment effect, which contributed to the 41% of the overall variation, but no significant difference among months (Table 4.4 B). Post-hoc tests indicated significant differences between the small transplant (Ts) and both the procedural control (Pc) and between the control (C) and the small transplant (Ts, Fig. 4.5 B).

Discussion

Effects of seaweed morphology on environmental variables

Canopy forming seaweeds often provide the dominant habitat on intertidal rocky shores, supporting rich invertebrate assemblages through the provision of living space and milder conditions beneath the canopies (Bruno and Bertness 2001; Wright et al. 2014; Umanzor et al. 2017). Here, we showed that the *Hormosira banksii* canopy *per se* provides cooler and

darker conditions compared to ambient but limited evidence that variation in *H. banksii* morphology and canopy cover affect the modification of abiotic conditions beneath the canopy. Despite this finding, there was also some evidence that different density and morphologies can influence the abundance of gastropods beneath or within canopies.

The density experiment did not show changes in temperature and light reduction with declining *H. banksii* density, going against the evidence that a decrease in canopy cover results in an increase of temperature (Coombes et al. 2013; Umanzor et al. 2017) and light levels (Wernberg and Toohey 2005; Tsatsumi and Wright 2016) beneath the canopies. The reasons for the lack of a density-effect in our experiment may relate to the way we measured these metrics (directly beneath the canopy) which suggest that even a small amount of *H. banksii* in quadrats (i. e. 25% cover) can affect light and sub-canopy temperature which may be ecologically relevant at the scale of small gastropods (Cartwright and Williams 2014).

We found temporal effects for the relative (percentage) reduction in temperature but not for light. The weaker reduction in temperature in February may reflect greater desiccation of thalli considering the time of the day when measurements were taken (midday) compared to early morning in March and April. However, the consistently large percentage reduction in light (> 80% reduction except for Ts in April) indicate the effectiveness of the *H. banksii* canopy in reducing light beneath the canopy, similar to other seaweed canopies that reduce light by for understory species (Reed and Foster 1984; Umanzor et al. 2017). For example, high density canopies of subtidal seaweed reduce benthic light by up to ~80%, with some species (e.g. *Desmarestia ligulata*) more efficient than others (e.g. *Macrocystis* and *Pterygophora*, Clark et al. 2004), showing how canopy density and seaweed morphology interact, resulting in a different amelioration of environmental conditions and provision of favourable habitats to associated species. Unfortunately, similar studies in the intertidal are scarce but show that density of canopies (Pocklington et al. 2019) affect the way how

canopy-forming seaweeds modify environmental conditions (bioengineer potential), accordingly to seaweed morphology and the time of the day when measures were taken (Umanzor et al. 2017).

In the morphology experiment we predicted that the small morph on the north coast would ameliorated abiotic conditions more strongly than the intermediate east coast morph because it has many branches and small vesicles (Mueller et al. 2015) that creates a thick mat that could potentially trap more water, reduce temperatures and decrease the rate of desiccation at low tide. However, the eastern *H. banksii* transplants were just as effective as the small north coast morph in buffering temperature and light. The large vesicles of the standard *H. banksii* may suffer less water loss than smaller vesicles (Bergquist 1959), possibly allowing the standard *H. banksii* to retain water and thus, reduce temperature beneath the canopies. Reductions in temperature and light increase with the density of canopies and species with more branches (e.g *Silvetia compressa*) are most able to shelter invertebrates (e.g. gastropod *Chlorostoma funebralis* (Umanzor et al. 2017). The similar reduction of temperature and light by both morphs may also be due to them having similar densities in our experiment. In the field, the east coast morph is typically at lower densities than the north coast morph (F. Gemelli personal observations), but we wanted to standardise density in the morphology experiment. Nevertheless, morphology treatments had a small contribution (~20%) to the overall temperature reduction, showing that within the same species, variation in the morphology may have a minor effect on the ability of seaweed to ameliorate environmental conditions.

Despite the similar reduction in temperature and light levels beneath canopies of different morphologies, in summer (February) we observed a lower temperature reduction compared to the other months, likely related to the daily variability in environmental conditions. As well, since we lost part of the cover in the translocation plots towards the end

the experiment (April), we didn't measure temperature and light beneath canopies in some plots, which explain the low values in temperature and light reduction (and percentage) in April.

Morphology and density effects on gastropods abundance

The modification of the physical environment by canopy-forming seaweeds with different morphology and cover can affect the occurrence of associated species, through the creation of habitat with different structure and conditions beneath the canopies. For example, dense stands of coralline seaweeds strongly reduce light availability and inhibit the growth of microbial films and epiphytes on which gastropods feed, causing a decrease in the diversity of both prey and predators (Kelaher 2003). Similarly, an increase in canopy cover protects gastropods from high temperature and irradiance during low tide, reducing the risk of desiccation (Umanzor et al. 2017). Thus, considering the small-scale spatial variability in the response of gastropods to different habitat (Beck 1998;2000), the effects of seaweed morphology and cover may vary according to seaweed identity and characteristics of associated species.

In our experiments, we observed a different response by the two species to the different morphology and density treatments. *Lunella undulata* did not occur beneath the east coast *H. banksii* morph while *C. odontis* colonized all morphology treatments. *Lunella undulata (Turbo undulatum,* Solander*)* is commonly found under the canopies of *H. banksii* or in crevices covered by the seaweed (Smoothey 2013) and in our experiments was more abundant beneath the high-density control canopies of the small morph compared to the transplants from the east coast. Given *L. undulata* is widespread on Tasmanian intertidal and subtidal rocky shores (Grove 2017), with the greatest abundance occurring on the east coast within the standard morph of *H. banksii* (Gemelli et al. 2018), the lack of colonization of this

morph was surprising. However, since only *L. undulata* from the north were tested in this experiment, it is possible they choose habitat differently to those on the east coast.

On low shores and mid-zone rock pools in New South Wales and Victoria, *L. undulata* was more abundant within beds of *Corallina officinalis* (Worthington and Fairweather 1989) and a standard morph of *H. banksii* (Povey and Keough 1991) similar to the one found on the east coast, than on bare rock. The high abundance of this species has previously been attributed to the food value of *C. officinalis* and the sheltered habitat provided by the higher structural complexity of *H. banksii* compared to bare substrata, where *L. undulata* was seldom found (Smoothey et al. 2013). In the lab, *L. undulata* from Tasmania readily feeds on *C. officinalis* (Gemelli pers. Obs.). At Beechford, coralline turf often creates an understory beneath the *H. banksii* canopy. However, to transplant the seaweed we scraped the turf to obtain a better attachment of the epoxy. Therefore, the higher abundance of *L. undulata* in the controls, where turf was present, support previous results and suggest an additive effect of coralline turf and *H. banksii* on their abundance on intertidal shores.

Chlorodiloma odontis (Wood, 1828) reached the greatest abundance beneath the control canopies, while more individuals colonized the large than the small *H. banksii* transplants. These patterns indicate that the presence of epoxy and ropes, an absence of *C. officinalis* as well seaweed morphology *per se* don't exert a strong influence on the colonization rate of the canopies by *C. odontis*. The greater colonization of the transplant than the translocation treatments observed in the last three experimental months, likely resulted from the minor loss of cover experienced by the large transplant respect the translocation during the experiment, resulting in the presence of more living space and shelter beneath the canopies, increasing the chances of survival (Olabarria and Chapman 2001), particularly smaller recruits.

Although the greatest abundance of *C. odontis* occurred within the high-density canopies, the similar abundance of *C. odontis* between the smaller canopies, particularly towards the end if the experiment, did not entirely support the hypothesis of a positive effect of canopy cover on abundance. However, most of the snails beneath the 50% and 25% canopy treatments were small recruits (shell size ~1 cm) and thus the greater number of branches and tiny vesicles of the small morph of *H. banksii* may have provided a good protection from physical variables or predation (Hayakawa et al. 2007b; 2008).

Other factors in addition to seaweed morphology and density may also be important in determining the abundance of gastropod species beneath the canopies of *H. banksii* including following conspecific trails (Chapman 1998) and size of snails (Smoothey 2013; Gemelli et al. unpublished data). Moreover, greater than 50% of the variation in the abundance of both species occurred on small spatial scales (among replicate quadrats separated by a few metres). It has been previously shown that large spatial variation occurs on small-scales on rocky intertidal shores (Underwood and Chapman 1996; Chapman 2005) and our study highlights that the density and morphology of intertidal seaweed are among multiple factors that may influence gastropod abundance. Nonetheless, here we showed that more than seaweed morphology and density alone, the interaction of these two factors with environmental conditions is likely to have a mixed, and perhaps additive effect on the abundance of intertidal gastropods. Future field and laboratory studies on the habitat choice of gastropods would be helpful in teasing apart the contribution of each of the above factors in influencing the abundance of gastropods that use *H. banksii* canopies as habitat.

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5 Chapter: Testing the contribution of seaweed morphology and biomass on the habitat choice of intertidal gastropods

Federica Gemelli, Craig R. Johnson, Simon Wotherspoon, Jeffrey T. Wright

Abstract

Species habitat choice is motivated by their specific needs for food and adaptation to both biotic and abiotic factors. In highly stressful environments such as the marine intertidal, where differences in the tidal cycles cause daily fluctuations in a range of abiotic stressors, species may be expected to select habitats with the mildest conditions and the greatest chances of survival. Ecosystem engineering canopy forming seaweed provide cooler, more humid and darker conditions beneath the canopies, reducing abiotic stress and consumer pressure. Gastropods are among the most common species found within seaweed canopies, but their abundance can vary greatly in relation to microhabitat availability and small-scale environmental conditions. Here, we investigated the behaviour and habitat choice of two gastropods, the Turbo *Lunella undulata* (Lightfoot, 1786) and Trochid *Chlorodiloma odontis* (W. Wood, 1828), for different morphs and cover of the fucoid *Hormosira banksii*. Laboratory trials, using pilot and choice experiments, were designed to understand whether the patterns observed in the field are driven by an active habitat choice of species relative to (1) seaweed morphology, (2) biomass and (3) external temperature. The experiments highlighted a species-specific interactive effect among temperature, seaweed morphology and biomass on the behaviour and habitat choice of both gastropods. Also, despite the limits of laboratory experiments, our results support previous field observations that gastropods don't have a clear preference for a specific *H. banksii* morph, reinforcing the evidence that variation in abiotic conditions, particularly temperature, influence the choice of habitat by intertidal gastropods.

Introduction

Species habitat choice has a strong influence on local abundance and the structure of biotic communities (Morris et al. 2003a). However, habitat selection may change over space and time due to habitat features (e.g. presence of pits, crevices, algal fronds, McCoy and Bell 1991; Gee and Warwick 1994; Beck 2000; Atilla et al. 2005), biotic interactions (competition and predation, Underwood 1984; Byers 2000; Klecka and Boukal 2014), environmental conditions (Jones et al. 1999; Wenger et al. 2018) and species age or body-size (Underwood 2004).

Intertidal rocky shores are physically challenging environments where organisms are exposed to strong, daily fluctuations in environmental conditions (e.g. temperature, desiccation stress) due to the rise and fall of tides (Denny and Whethey 2001). As a result, mobile species such as gastropods move actively on the shore often choosing cool places (Garrity 1984; Williams and Morritt 1995; Underwood and Chapman 1996) to limit thermal and desiccation stress (McQuaid et al. 1988, Bates and Hicks 2005), avoid predators (Connell 1961) and forage (Owen-Smith et al. 2010; Chapperon and Seuront 2011a).

Canopy forming seaweeds modify physical conditions such as temperature, humidity (Jurgens and Gaylord 2018) and light (Reed and Foster 1984; Wernberg et al. 2005), beneath the canopies and are colonized by many gastropod species which use the canopies for both habitat and feeding (Pardo et al. 2004; Cartwright et al. 2012; Rickards et al. 2015). The abundance of gastropods colonizing canopies may vary between sites that differ depending on algal morphology (Chemello and Milazzo 2002) and canopy cover (Schiel and Lilley 2007; Umanzor et al. 2017). For instance, the turban snail *Chlorostoma funebralis* occurred at high densities at low tide beneath dense canopies of the leathery seaweed *Silvetia compressa* compared to seaweed with a corticated (*Chondracanthus canaliculatus*) and foliose (*Pyropia perforata*) morphology (Umanzor et al. 2017). As well, larvae of the *Turbo (Batillus)*

cornutus settled preferably to fragments of seaweeds with a more complex thallus architecture (*Marginisporum crassissima* and *Gelidium elegans*) compared to species with a foliose morphology (e.g. *Ulva pertusa*), demonstrating that algal morphology can be important for different life-cycle stages (Hayakawa et al. 2007).

Despite within-species variability in morphology and density being common in canopy-forming seaweeds (De paula and Oliveira 1982; Blanchette 1997; Wright et al. 2004), we know little about how these factors influence habitat choice of gastropod species from different sites with different environmental conditions. To evaluate the importance of these different factors in providing favourable habitat, a careful evaluation of gastropod behaviour for different habitats when presented alone and in combination (choice) as well as incorporating important abiotic variables is required (Burnaford 2004).

In Tasmania, Australia, the Turbo *Lunella undulata* and the Trochid *Chlorodiloma odontis* are two of the most abundant gastropod species on intertidal shores. Both species are commonly associated with the habitat-forming intertidal seaweed *Hormosira banksii* Turner (Decaisne), which occurs as different morphologies on the north and east coasts of Tasmania (Mueller et al. 2015; Gemelli et al. 2018). On the north coast, which has a high tidal amplitude, semi-diurnal tidal regime and is exposed to low wave energy, *H. banksii* has a small, highly branched thallus and forms dense canopies that often cover 100% of the substratum. In comparison, on the east coast, which has a diurnal tidal regime and greater wave energy, density tends to be lower and thalli larger and the overall morphology is similar to those found on rocky shores of mainland Australia and New Zealand (Mueller et al. 2015, Gemelli et al. 2018). The abundance of *L. undulata* and *C. odontis* varies between regions and sites with *L. undulata* more abundant on the east coast and *C. odontis* on the north coast. Moreover, the two species appear to use *H. banksii* habitat differently with *L. undulata*

usually occurring attached to vesicles of the *H. banksii* or beneath the canopies and *C. odontis* usually only attached to *H. banksii* branches and vesicles.

Despite the evidence of a positive influence of *H. banksii* morphological traits, particularly vesicle size, on the abundance of associated gastropods (Bishop et al. 2009; 2013), which appears to partially explain the different patterns of abundance for these two species (Gemelli et al. 2018), habitat choice may be influenced by other factors including differences in responses to environmental conditions at different scales (e.g. region and site). Here, we set up a series of pilot and choice laboratory experiments for *L. undulata* and *C. odontis* collected from the two regions (north v. east), where distinct *H. banksii* morphs occur to tease apart the influence of these factors on the behaviour and habitat choice for these two species. Specifically, we examined (1) whether seaweed morphology (habitat quality) and (2) biomass (habitat quantity) influenced habitat choice of gastropods and how habitat choice changed with the region of origin for gastropods and temperature.

Material and Methods

Collection of snails and habitat

Lunella undulata and *Chlorodiloma odontis* (~100 for each species) and seaweed fronds (~100) were collected from one northern site (Beechford, 41°01'22" S, 146°56'39" E) and one eastern site (Shelly Beach, 42°34'0 05" S, 147°53'17.5" E) at the end of summer 2018. Initially, forty snails (twenty for each species) were placed in the same aerated tank and left at room temperature (~22 C°), but both species died in a couple of days. Thus, more gastropods and seaweed fronds were collected and placed separately into 20L aquaria (26.5cm x 39cm x 24.5cm) at 15°C on a 12:12 light cycle. Gastropods were also provided with a bed of mix coralline turf algae and particles on the bottom of the tank for feeding. Aeration and water circulation were provided using air stones. To set each experiment,

gastropods were randomly taken from the holding tanks and then returned prior to setting up new experiment.

Pilot experiment

Given that the behaviour of species may differ under artificial conditions, we initially tested whether both *L. undulata* and *C. odontis* used *H. banksii* as habitat in the laboratory under simulated low tide conditions. Ten snails of either *L. undulata* or *C. odontis* were placed in the centre of a tray (75 x 435 x 315 mm) filled with a small amount of seawater (~2 cm), which left all gastropods partially exposed to air. The amount of water was chosen accordingly to the behaviour of gastropods observed in the field. There, gastropods became active in presence of small amounts of water on the rocks but withdrawn in the shell closing the opercula when left in dry conditions. For the experiment, one side of each tray had 200 g (~33% cover of the bottom of the tray) of *H. banksii* placed on the bottom and snails were left free to choose between bare space and the seaweed. After 90 minutes we counted all the snails attached or beneath the seaweed canopies and on the bare space or walls of the trays. The response of both gastropods was tested separately for both the small and standard *H. banksii* morphs using snails from both the north and east coasts (but only tested against the morph from each region). After observing the motility behaviour of each species under different temperatures, all experiments were done at ~15˚ and ~21˚ (air temperatures within the range of summer and winter in Tasmania), at which gastropods were active moving and able to choose a specific habitat, to understand if temperature has any effect on the response of gastropods. Each experiment was replicated six times.

Choice experiments

Effect of H. banksii morphology (Habitat quality effect)

The habitat choice of *L. undulata* and *C. odontis* for the two *H. banksii* morphs was examined in choice experiments. As for the pilot experiments, ten snails of a single species were placed

in the centre of trays. 200 g of the small (north) and standard (east) *H. banksii* were placed either side of each tray and snails were left to choose among the bare space in the centre and the two *H. banksii* morphs. After 90 minutes we counted the number of snails found within the different habitats and assigned them to the following categories: bare space (B), small *H. banksii* (SH) and standard *H. banksii* (STH). The habitat choice of both gastropods for the different morphs was tested separately using snails from different regions (north v. east) and done at two temperatures (15° v. 21°). The experiment was replicated six times for each gastropod species/ region/ temperature combination.

Effects of H. banksii biomass (Habitat quantity effect)

The effect of different seaweed biomass on the habitat choice of *L. undulata* and *C. odontis* was also tested. Trays (with ~2 cm of water), containing 200g (large), 100g (medium) and 50 g (small) amounts of a single *H. banksii* morph were established to create different biomass categories. The approximate percentage cover of these three biomasses was ~33%, ~15% and ~7%. Ten individuals of *L. undulata* or *C. odontis* were placed in the centre of trays and snails left to choose among the different habitats. After 90 minutes we counted the snails within each habitat and assigned them to the following categories: bare space (B), large (200 g), medium (100 g) and small (50 g). Experiments for both gastropods were done for both morphs of *H. banksii*, with snails originating from different regions (north v. east) and done at two temperatures (15° v. 21°). Again, the experiment was replicated six times.

Statistical analysis

All statistical analyses were performed using the R-2.6.2 (R Development Core Team, 2008) computer package. Generalized linear models were used to test the a priori predictions about influence of seaweed morphology and biomass relative to the region of origin and temperature on the behaviour and habitat choice of gastropod species. Full saturated models following Poisson distribution, were used for each experiment and the most parsimonious

model was derived by backward selection examining the change in the likelihood ratio (G^2) with ANOVA. Terms were only removed from the model if doing so did not result in a significant increase in the Akaike Information Criterion (AIC, Akaike 1973), after comparing all the different models. The most parsimonious model had the smallest AIC value (Anderson et al. 2008) and included the set of predictor variables which explained the largest amount of variation. Correspondence analysis (CA) was used to explore the variability in the response of gastropod across each of the different habitat. Correspondence analysis is a multivariate technique to represent associations in two-way contingency tables. When presented graphically the rows and columns are plotted in a joint plot, represented by points on the graph, which position indicate the strength of the association between variables (Agresti 2002; Quinn and Keough 2002).

Results

Pilot experiment

In the pilot experiment, for both species the proportion of snails colonizing *H. banksii* was significantly higher than the snails choosing bare space, but gastropod's habitat choice changed between species accordingly to external temperature (Tables 5.1 A-D, Figs.5.1 A-D).

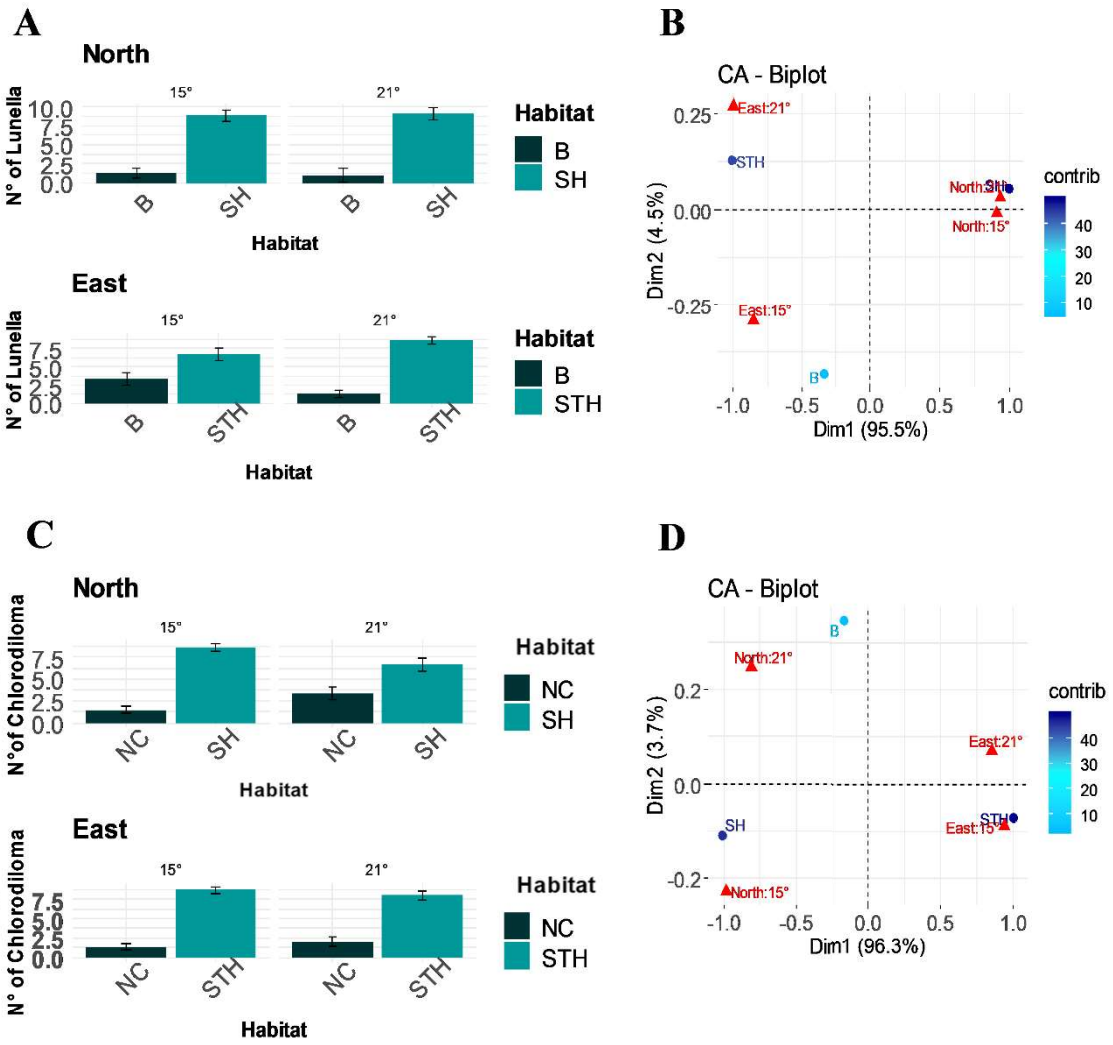
Table 5.1 A-D. (A) ANOVA of the minimal adequate model (GLM) testing the association of *Lunella undulata* from the north (A) and east (B) and *Chlorodiloma odontis* from the north (C) and east (D) with a specific *Hormosira banksii* morphology depending on ambient temperature (15 C° and 21 C°). Just the final model and significative factors were reported here. Abbreviations: Ha = Habitat, Re = Region.

A	Df	Deviance Resid.	Df	Resid. Dev	Pr(>Chi)
Ha	1	84.03	22	31.98	< 0.001

B	Df	Deviance Resid.	Df	Resid. Dev	Pr(>Chi)
Ha	1	35.97	22	27.67	< 0.0001
Ha x Te	1	6.88	20	20.79	0.008

C	Df	Deviance Resid.	Df	Resid. Dev	Pr(>Chi)
Ha	1	33.63	22	19.83	< 0.0001
Ha x Te	1	5.61	20	14.22	0.01

D	Df	Deviance Resid.	Df	Resid. Dev	Pr(>Chi)
Ha	1	58.22	22	14.20	< 0.0001



Figures 5.1. A-D) Abundance of *Lunella undulata* (A) in bare space (B) and the small (SH) or standard (STH) *Hormosira banksii* from two regions (north and east) at two temperatures (15 C° and 21 C°). Correspondence analysis of abundance of *L. undulata* (B) from two regions at two temperatures among different habitats as function of the first two axes. Abundance of *Chlorodiloma odontis* (C) between bare space and the small (SH) or standard (STH) *Hormosira banksii* from two regions (north and east) at different temperatures (15 C° and 21 C°). Correspondence analysis of abundance of *Chlorodiloma odontis* (D) from two regions at two temperatures among different habitats as function of the first two axes. Red triangles indicate snails from the east or north coast tested at either 15 or 21°C. Dark blue circles indicate the different *H. banksii* morphs. Aqua circles indicate the habitat with the lowest contribution.

For *L. undulata* from the north, there was a significant effect of habitat but not temperature (Table 5.1A, Fig. 5.1 A upper panel). Instead, for eastern snails there was a

stronger effect of habitat and temperature (Table 5.1 A, Fig. 5.1 A bottom panel), which colonized more *H. banksii* with increasing with temperature. The correspondence analysis (CA, Fig. 5.1 B, right panel) highlighted the different effect of temperature, with *L. undulata* from different regions separated along dimension two and suggesting a close association of *L. undulata* with *H. banksii*. Along the same dimension, eastern *L. undulata* separated according to temperature but northern snails did not, suggesting that the choice of eastern snails for *H. banksii* as habitat would be more affected by external temperature.

For *C. odontis* there was a significant habitat x temperature (Table 5.1 C-D) for northern snails, reflected by the higher colonization rate of *H. banksii* at cool temperatures (Fig. 5.1 C upper panel). Instead, eastern snail's choice was affected just by habitat, with snails choosing more *H. banksii* than bare space (Fig. 5.1 C bottom panel). In the correspondence analysis (Fig 5.1 D) *C. odontis* from different regions were separated along dimension two but, in contrast to *L. undulata,* northern snails separated according to temperature whereas eastern snails did not, suggesting the choice of northern *C. odontis* for *H. banksii* as habitat was more affected by temperature.

Choice experiments

Effect of Hormosira banksii morphology

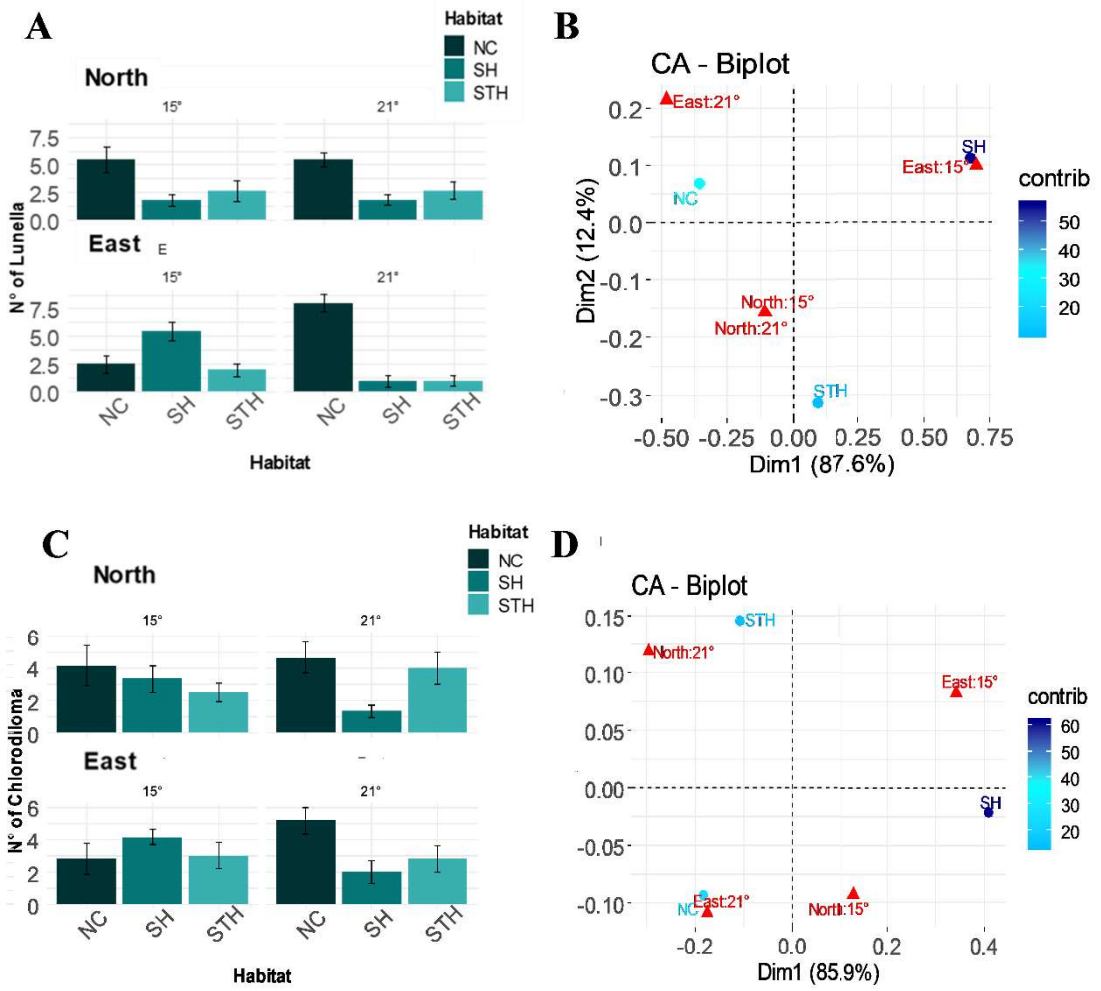
In the morphology choice experiment, gastropods colonized *H. banksii* morphs in different proportions, according to the region of origin and temperature. For *L. undulata* there was a significant habitat x region x temperature effect (Table 5.2 A). However, temperature more strongly affected the choice of eastern v. northern snails, with more eastern *L. undulata* choosing the small *H. banksii* compared to the other habitats only at 15°C (Fig. 5.2 A). The habitat choice of snails originating from the north did not differ between morphs and this was unaffected by temperature. Correspondence analysis (Fig. 5.2 B) highlighted this region-

specific effect of temperature on eastern snails, with eastern *L. undulata* more separated along dimension one than northern snails.

Table 5.2 A-B. ANOVA testing the association of *Lunella undulata* with different *Hormosira* banksii morphologies depending on the region of origin (north and east) and temperature (15 C° and 21 C°). Just the final model and significative factors were reported here. Abbreviations: Ha = Habitat, Re = Region, Te = Temperature.

A	Df	Deviance Resid.	Df	Resid. Dev	Pr(>Chi)
Ha	2	43.18	69	133.16	< 0.0001
Ha x Re	2	8.84	65	124.32	0.012
Ha x Te	2	21.63	63	102.68	< 0.0001
Ha x Re x Te	2	18.95	60	83.526	< 0.0001

B	Df	Deviance Resid.	Df	Resid. Dev	Pr(>Chi)
Ha	2	8.55	69	105.12	0.013
Ha x Re	2	1.71	65	103.41	0.42
Ha x Te	2	13.60	63	89.80	0.001



Figures 5.2 A-D. Abundance of *Lunella undulata* (A) within different habitats (bare space (B), small (SH) and standard (STH) *Hormosira banksii*) from two regions (north and east) at different temperatures (15 C° and 21 C°). Correspondence analysis of abundance of *Lunella undulata* (B) from two regions at two temperatures among different habitats as function of first two axes. Abundance of *Chlorodiloma odontis* (C) within different habitats (bare space (B), small *Hormosira banksii* (SH and standard *Hormosira banksii* (STH)) from two regions (north and east) at different temperatures (15 C° and 21 C°). Correspondence analysis of abundance of *Chlorodiloma odontis* (D) from two regions at two temperatures among different habitats as function of first two axes. Red triangles indicate snails from the east or north coast tested at either 15 or 21°C. Dark blue circles indicate the different *H. banksii* morphs. Aqua circles indicate the habitat with the lowest contribution.

For *C. odontis* the minimal adequate model found a strong association between habitat x temperature (Table 5.2 B), reflecting the greater colonization of the small *H. banksii* at 15°C and the opposite pattern at 21°C (Fig. 5.2 C). The correspondence analysis (Fig. 5.2 D) indicated *C. odontis* from different regions occurred in opposite panels along dimension two, depending on temperature. The greater separation between snails exposed to the warm than cool temperatures, suggested a stronger influence of the first condition on the choice of *H. banksii* by *C. odontis*.

Effects of H. banksii biomass

In the habitat quantity experiment, the habitat choice of *L. undulata* and *C. odontis* in the presence of different biomass of *H. banksii* varied between species and was influenced by seaweed morphology, temperature and region.

For *L. undulata* in response to the small *H. banksii* morph, there was a significant habitat x region x temperature interaction (Table 5.3 A), reflecting higher colonization of the small *H. banksii* at 21°C than 15°C, particularly by eastern snails (Fig. 5.3 A). Correspondence analysis (Fig. 5.3 B) highlighted the different effect of temperature on the habitat choice of *L. undulata* between regions, with snails from the two regions separated along dimension two accordingly to temperature. The separation was greater for eastern than northern snails, which colonized more the full canopies at warmer temperatures (Fig. 5.3 B). Instead, at cooler temperatures northern snails chose bare space over *H. banksii*, highlighting a different effect of temperature on the habitat choice of snails from different regions.

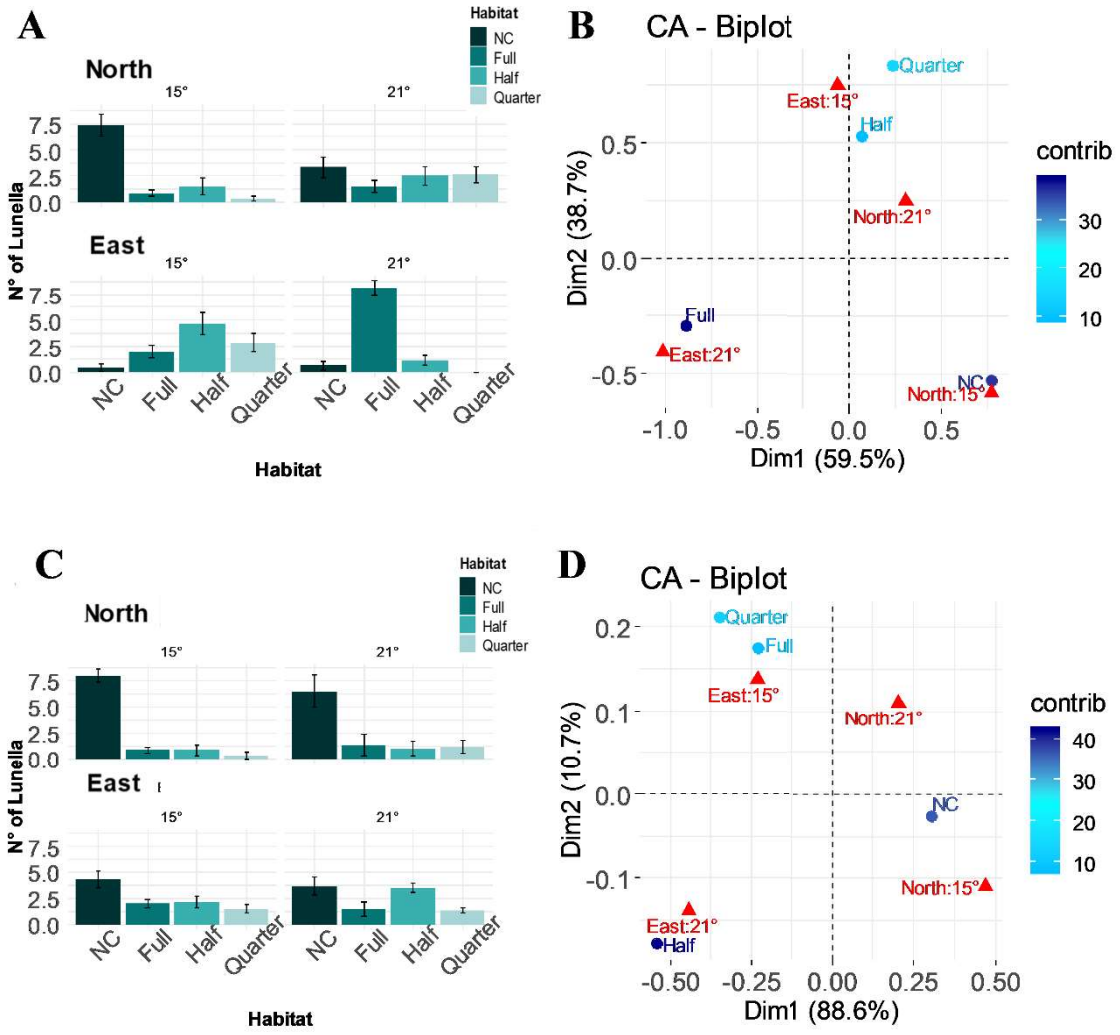
In comparison, in the presence of the standard *H. banksii* there was no clear effect of *H. banksii* biomass on the habitat choice of *L. undulata*. The minimal adequate model to explain the distribution of *L. undulata* found a strong association between habitat x region (Table 5.3 B), reflected by the greater colonization of *H. banksii* over bare space by eastern than northern snails. Correspondence analysis (Fig. 5.4 B) highlighted these differences with

snails occurring in opposite panels along dimension one. Also, the greater distance along dimension two between snails from the same region exposed to different temperatures, highlighted the stronger effect of this factor on the choice of *L. undulata*, particularly at 21°C.

Tables 5.3 A-B. ANOVA testing the association of *L. undulata* with different biomass of the small *H. banksii* (A) depending on the region of origin (north and east) and temperature (15 C° and 21 C°). Just the final model and significative factors were reported here. ANOVA testing the association of *Lunella undulata* with different biomass of the standard *Hormosira banksii* (B) depending on the region of origin (north and east) and temperature (15 C° and 21 C°). Just the final model and significative factors were reported here. Abbreviations: Ha = Habitat, Re = Region, Temperature = Te.

A	Df	Deviance Resid.	Df	Resid. Dev	Pr(>Chi)
Ha	3	17.66	92	280.82	< 0.0001
Ha x Re	3	86.56	87	194.26	< 0.0001
Ha x Te	3	35.39	84	158.87	< 0.0001
Re x Te	1	12.84	83	146.02	< 0.0001
Ha x Re x Te	3	37.33	80	108.69	< 0.0001

B	Df	Deviance Resid.	Df	Resid. Dev	Pr(>Chi)
Ha	3	110.95	92	155.54	< 0.0001
Ha x Re	3	28.16	87	127.38	< 0.0001



Figures 5.3 A-D. Abundance of *Lunella undulata* (A) among different habitats (bare space (B), large (Full), medium (Half) and small (Quarter) biomasses of the small *Hormosira banksii* from two regions (north and east) at different temperatures (15 C° and 21 C°). Correspondence analysis of abundance of *Lunella undulata* (B) from two regions at two temperatures among the different habitats as function of first two axes. Abundance of *L. undulata* (C) within different habitats (bare space (B), large (Full), medium (Half) and small (Quarter) biomasses of the standard *H. banksii* from two regions (north and east) at different temperatures (15 C° and 21 C°). Correspondence analysis of abundance of *L. undulata* (D) from two regions at two temperatures among the different habitats as function of first two axes. Red triangles indicate snails from the east or north coast tested at either 15 or 21°C. Dark blue circles indicate the different *H. banksii* morphs. Aqua circles indicate the habitat with the lowest contribution.

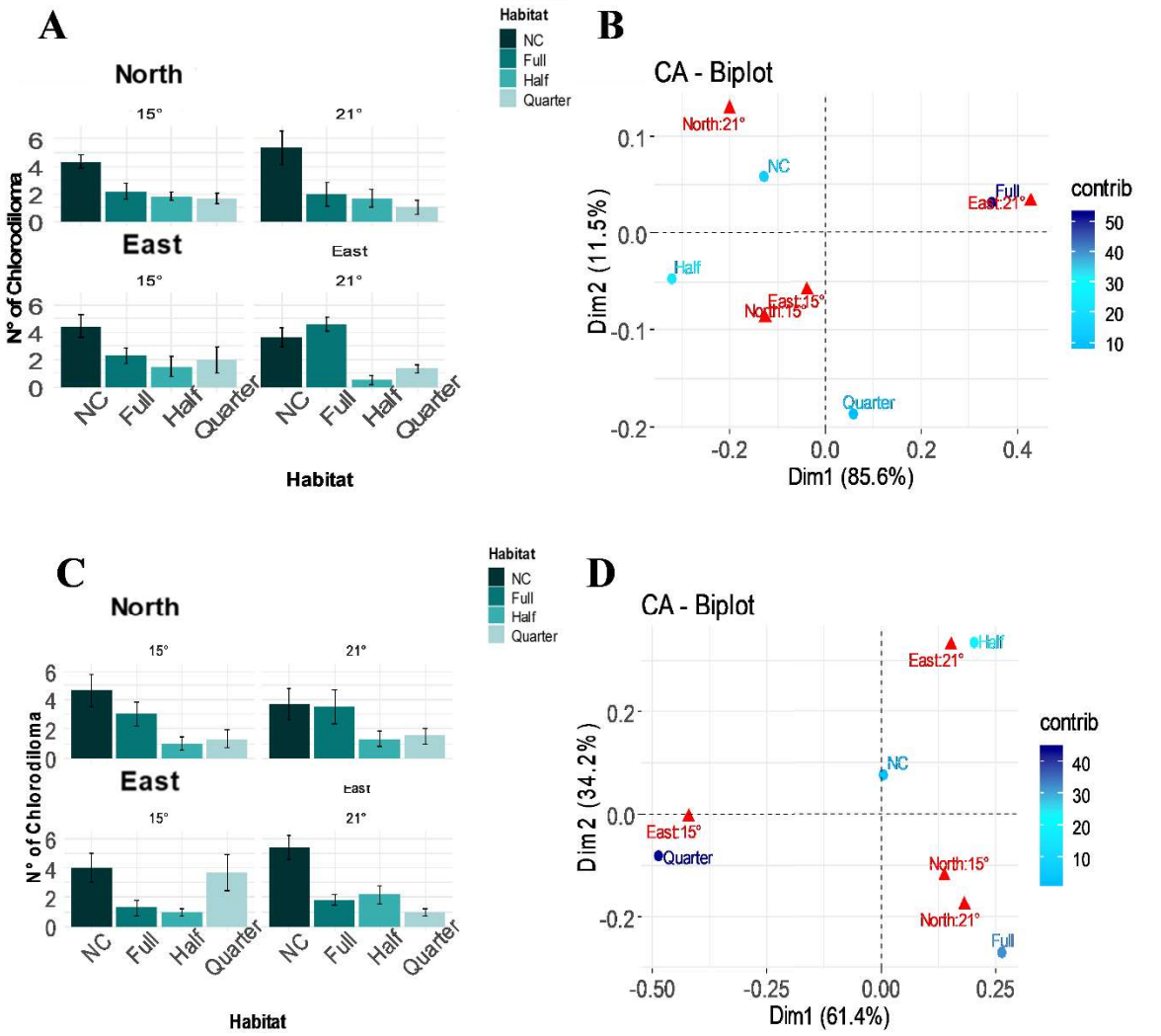
The habitat choice of *C. odontis* to different biomass of *H. banksii* varied between the two seaweed morphs. In the presence of the small *H. banksii* morph, a weak habitat x region association (Table 5.4 A) occurred which reflected the small differences in colonization between northern and eastern snails (Fig. 5.4 A). Despite the absence of a significant effect, temperature appeared to have a weak influence on the habitat choice of *C. odontis*, particularly eastern ones, which colonized more *H. banksii* at warm than cool temperatures. Correspondence analysis (Fig. 5.4 B) highlighted these patterns, with *C. odontis* from the same regions separated along dimension two and eastern snails at 21°C laying close to full canopies at and northern ones close to bare space.

In the presence of the standard morph of *H. banksii* (Fig. 5.4 C) biomass affected the choice of *C. odontis* accordingly to temperature and region of origin. The minimal adequate model found a weak association among habitat x region x temperature, but a stronger one between habitat x region (Table 5.4 B), reflecting the different colonization of each biomass treatment by snails from different regions as well as a weak effect of temperature at small scale (region). High temperature affected northern *C. odontis* more than eastern *C. odontis*, which colonized more *H. banksii* than bare space. Correspondence analysis (Fig. 5.4 D) highlighted the strong regional x temperature variability in the habitat choice of *C. odontis*, with eastern snails laying in opposite panels along dimension one. However, northern snails at both temperatures occurred close along both dimensions highlighting a consistent choice for the large biomass of *H. banksii*.

Table 5.4 A-B. ANOVA testing the association of *Chlorodiloma odontis* with different biomass of the small *Hormosira banksii* (A) depending on the region of origin (north and east) and temperature (15 C° and 21 C°). Just the final model and significative factors were reported here.
ANOVA testing the association of *Chlorodiloma odontis* with different biomass of the standard *Hormosira banksii* (B) depending on the region of origin (north and east) and temperature (15 C° and 21 C°). Just the final model and significative factors were reported here. Abbreviations: Ha = Habitat, Re = Region, Tmperature = Te.

A	Df	Deviance Resid.	Df	Resid. Dev	Pr(>Chi)
Ha	3	55.82	92	122.97	< 0.0001
Ha x Re	3	6.77	87	116.18	0.07

B	Df	Deviance Resid.	Df	Resid. Dev	Pr(>Chi)
Ha	3	46.32	92	157.12	< 0.0001
Ha x Re	3	11.6	87	145.46	0.008
Ha x Te	3	8.24	84	137.22	0.04
Ha x Re x Te	3	6.93	90	130.09	0.07



Figures 5.4 A-D. Abundance of *C. odontis* (A) within different habitats (bare space (B), large (Full), medium (Half) and small (Quarter) biomasses of the small *H. banksii* from two regions (north and east) at different temperatures (15 C° and 21 C°). Correspondence analysis of abundance of *C. odontis* (B) from two regions at two temperatures among the different habitats as function of first two axes. Abundance of *Chlorodiloma odontis* (C) within different habitats (bare space (B), large (Full), medium (Half) and small (Quarter) biomasses of the standard *Hormosira banksii* from two regions (north and east) at different temperatures (15 C° and 21 C°). Correspondence analysis of abundance of *Chlorodiloma odontis* (D) from two regions at two temperatures among the different habitats as function of first two axes. Red triangles indicate snails from the east or north coast tested at either 15 or 21°C. Dark blue circles indicate the different *H. banksii* morphs. Aqua circles indicate the habitat with the lowest contribution.

Discussion

Lunella undulata and *Chlorodiloma odontis* almost always chose *H. banksii* in the pilot experiment, rapidly colonizing the canopies, where they remained for its duration. Similarly, in the field both species were observed inactive beneath the canopies at low tide and moving just with rising tides. These observations support previous studies on the habits of gastropods to spend most of their time in habitats where they survive well (Olabarria et al. 2001) and moving out to feed, reproduce or in response to environmental cues (e.g. rising tides, Alfaro 2006). However, the different response of the two species to temperature, either in presence of different *H. banksii* morphs and different biomasses, suggest that the choice of *H. banksii* as a habitat by each species is influenced by numerous factors.

Temperature and humidity are considered to be among the most important determinants of organismal distribution in the intertidal zone (Helmuth and Hofmann 2001). At low tide during exposure to air, factors such as wind speed and solar exposure, can increase thermal and desiccations stress (Johnson 1975; Helmuth and Hoffmann 2001). Although these laboratory experiments lack these factors, the different behaviour of both species, when at different temperatures support the hypothesis of an influence by this factor on the observed patterns. As well, the strong effect of temperature detected in the pilot experiment for eastern *L. undulata* and northern *C. odontis* which both colonized more *H. banksii* at warm (21 C°) and cool (15 C°) temperatures respectively, suggested a different thermal tolerance for the two species, which likely reflect the differences in environmental conditions between the north and east coast of Tasmania.

The north coast is exposed to higher tidal amplitudes (Short 2006a) and a semidiurnal tidal regime, which is likely to result in greater fluctuations in temperature (Mueller et al. 2015) and likely a higher risk of desiccation for intertidal species at low tide (R. Lewis unpublished data). Thus, the difference in the proportion of *C. odontis* and *L. undulata* not

choosing *H. banksii* according to temperature and region of origin, are consistent with the hypothesis that abiotic factors at small scales may influence habitat choice of species (Williams and Morritt 1995; Jones and Boulding 1999; Burnaford 2004; Cartwright and Williams 2012).

The colonization of both *H. banksii* morphs in the choice experiment support the hypothesis of an influence of environmental factors as temperature on the habitat choice of gastropods (Chapperon and Seuront 2012) and suggest that seaweed morphology *per se* can influence the habitat choice of gastropods depending on the species and their region/habitat of origin (Crowe 1996, Crowe and Underwood 1999). The habitat choice of *L. undulata* in presence of different seaweed morphs was less affected by temperature, with northern snails colonizing almost equally the two *H. banksii* morphs and eastern snails choosing the small *H. banksii* morph over the standard morph at lower temperature and bare space at warmer temperatures (Fig.2A). Likely, the different behaviour of *L. undulata* accordingly to temperature, results from an intrinsic (e.g. genetic or learned, Crowe and Underwood, 1999) adaptation to the conditions of the region of origin, and support the evidence that the ability of *H. banksii* to reduce temperature beneath the canopies (Chapter 4, R. Lewis unpublished data) is important in the provision of moist and shelter to *L. undulata* (Worthington and Fairweather 1989)

In contrast to *L. undulata*, the behaviour of *C. odontis* did not differ between regions and snails colonized the small morph more at cool temperatures and the standard morph at warmer ones. The colonization of both seaweed morphs by *C. odontis* is consistent with our field observations and experiment (Chapter 4), where northern *C. odontis* colonized both *H. banksii* morphs. Considering that the different *H. banksii* morphs reduced temperature to similar levels (Chapter 4) and that intertidal gastropods have often a body temperature close to their thermal limit (Somero 2002), the slight difference in the colonization of the two

seaweed morphs by *C. odontis* depending on temperature, suggest that even a small temperature reduction by *H. banksii* may influence the habitat choice of *C. odontis*. However, at this stage we are not able to attribute these differences exclusively to temperature, because laboratory conditions do not accurately replicate the behaviour of gastropods in the field (Connell 1961; Chapman 2000; Olabarria et al. 2001). Nonetheless, the results from this experiment clearly show that the morphology of *H. banksii* alone does not strongly affect the choice of gastropods (Chapter 2), suggesting instead a combination of temperature and seaweed morphology in determining the observed patterns.

The effect of biomass on the habitat choice of gastropods varied between species and depended on seaweed morphology, temperature and region of origin. For *L. undulata,* the effect of biomass was stronger in presence of the small vs. the standard *H. banksii*. In presence of the small morph, eastern *L. undulata* readily colonized the canopies, particularly with increasing temperature, while northern snails chose almost equally the different biomass habitats at warm temperature and chose the bare space more than *H. banksii* at cool temperatures. Similar patterns occurred in presence of the standard morph, with the difference that northern snails chose the bare space more under both temperature conditions. Field studies showed that *L. undulata* prefers moist, seaweed covered habitats (Worthington and Fairweather 1989) where they hide seeking protection against wave action, desiccation and predation. However, the higher proportion of snails choosing bare space than *H. banksii* at low temperatures suggest a different behaviour of *L. undulata* in relation to thermal conditions. Cool temperature appears to decrease the strength of association between ecosystem engineers and intertidal species (Burnaford 2004; Cartwright and Williams 2014), while warm temperatures lead to an increase in the choice of shaded habitats (Cartwright and Williams 2012). Thus, the differences found in the habitat-choice of *L. undulata* may be related to the capacity of a different capacity of each *H. banksii* morph to retain water and

provide moist to snails at warm temperatures and as well, to the habit of *L. undulata* to aggregate, which decreases water loss (McMahon 1990, Muñoz et al. 2008) allowing snails to slow the rate of water loss when exposed to air may explain why snails didn't always choose *H. banksii*.

For *C. odontis*, the decreasing abundance of snails among habitats of different biomass support field results and previous studies on the positive influence of habitat quantity on species abundance (Attrill et al. 2000; Torres et al. 2015). As well, the greatest colonization of the large canopies of *H. banksii* by snails with increasing temperature, is consistent with the positive effect of canopy cover on the reduction of temperature (Beerman et al. 2013; Umanzor et al. 2017) and the hypothesis that gastropods would select more protective microhabitats under stressful conditions (e.g. raising temperatures Jones and Boulding 1999). Therefore, an increase in seaweed biomass, is likely to increase the potential of *H. banksii* to buffer temperature, with the effects varying between species from different regions (Crowe and Underwood 1999).

Accordingly, we observed a stronger effect of warm temperature on the habitat choice of eastern than northern *C. odontis* just in presence of different biomass of the small *H. banksii* morph. These patterns suggest a lower tolerance to desiccation stress of snails from this region, which remain exposed to air for shorter time than northern snails. Likely, greater biomass of the small *H. banksii*, able to trap more water thanks to the bushy structure represent a better thermal refuge than the standard *H. banksii* morph for these snails. An alternative hypothesis is that *C. odontis* may follow conspecific trails (Chapman 1998), although this behaviour has not been documented for *C. odontis.*

Overall, despite the evidence that biomass more than seaweed structural complexity influence the abundance of associated species (Attrill et al. 2000; Parker et al. 2001; Cacabelos et al. 2007; Torres et al. 2015) and that a large morph of *H. banksii* increases the

abundance of gastropods in estuaries (Bishop et al. 2009; 2013), here we suggest that the effect of *H. banksii* morphology and biomass vary with temperature and region of origin of snails. Both these parameters in turn affect the ability of *H. banksii* to provide microhabitats of different complexity and reduced temperatures beneath the canopies. Thus, the habitat choice by gastropods is likely to be influenced by an interplay among seaweed morphology, biomass and temperature, in relation to the adaptations of gastropods to the conditions at local scales. Despite additional factors likely influencing the behaviour and habitat choice of the gastropod species, our study represents the first attempt of a comprehensive investigation on the utilization of *H. banksii* as habitat by gastropod species in Tasmania.

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Chapter 6: *Hormosira banksii* as an ecosystem engineer on Tasmanian intertidal shores: a synthesis

In this thesis, descriptive and manipulative studies were used to explore the link between different *H. banksii* morphologies and the structure of understorey communities, with particular focus on how morphology and canopy density affect the seaweed bioengineer potential across different habitats and the consequences for gastropod species which use the canopies as habitat.

I found large morphological variation in *H. banksii* morphological traits between different habitats and at different times (Chapter 2). Intertidal seaweeds typically have a high functional trait plasticity in response to physical factors as temperature, light, nutrients and wave exposure (Blanchette 1997; Fowler-Walker et al. 2006; Eggert 2012; Mabin et al. 2013; Flukes et al. 2014). Therefore, a quantitative analysis of the scales at which seaweed morphology and environmental conditions may differ (Coleman and Muhlin 2008) was imperative to evaluate patterns (Underwood and Chapman 1996; Burrows et al. 2009) that may determine their effects, both at small and large scales, on the structure of associated communities in the intertidal zone.

I found the broadest variation in seaweed morphology across habitats (coasts vs. estuaries) and regions (north vs. east) with different environmental conditions. Differences in wave exposure (Ralph et al. 1999) and tidal regime (Mueller et al. 2015) have been reported to contribute to the phenotypic variation of this species. In particular, on the north coast of Tasmania, where emersion times are greater than the east coast (Mueller et al. 2015), a short bushy *H. banksii* morph occurs, with short thalli and a high number of branches and small vesicles. On this coast, individuals often grow close together to create a tight structure that reduces the effects of extremes in temperature and irradiation at low tide (R. Lewis unpublished data) beneath the canopy.

Hormosira banksii thalli are flexibile and have a low whiplash effect, which has been reported to have a negative effect on understory species in other intertidal seaweed (Leonard 1999; Hancock and Petraitis 2001). Instead at low tide, seaweed canopies lay flat creating a relatively cool, moist habitat for understory species at low tide. Thus *H. banksii* is likely to have more positive than negative effects on association species, providing habitat and shelter from abiotic and biotic stress (e.g. high temperature, predation). In particular, the highly branched *H. banksii* may trap water, keeping it moist for long periods of time and reduce thermal stress for associated gastropods. Also, as the northern *H. banksii* provide habitat and shelter, the larger size of *H. banksii* on the east coast and estuaries, increase the amount of hard surface for gastropod attachment and biofilm grows, on which gastropods feed (Bishop et al. 2009; 2013).

Previous studies found rich invertebrate communities and the greatest mollusc abundance within canopies of highly-branched seaweed (Beck 1998; Chemello and Milazzo 2002; Schagerström et al. 2014) and diverse macroalgal communities (Best et al. 2014), due to the reduction in temperature and desiccation at low tide and provision of a refuge from predators. Accordingly, we found the greatest diversity of gastropods associated with the small *H. banksii*, but an overall low contribution (15%) of the seaweed morphological traits to the patterns of gastropod abundance. Interestingly, gastropod abundance resulted positively correlated with different *H. banksii* traits in a specific habitat, suggesting that the variation in a single morphological trait contribute differently the abundance of species accordingly to the abiotic environment (e.g. temperature reduction) where species occur. Indeed, there is strong evidence of the facilitative role exerted by intertidal seaweeds in providing milder conditions beneath the canopies (Wright et al. 2014; Scrosati and Ellrich 2018) and increasing the numbers of available niches (Attrill et al. 2000).

Generally, invertebrate species using seaweeds and seagrasses as habitat are not specialized to species, responding more broadly to the food and refuge value offered (Duffy and Hay 1991). We found great difference in the abundance of gastropod species across sites, habitats and regions, but two dominant species were found within or beneath the canopies of *H. banksii* with different morphology. The Turbo *Lunella undulata* (Lightfoot, 1786) colonized both the northern (small) and eastern (standard) seaweed morphs, while the Trochid *Chlorodiloma odontis* (W. Wood, 1828) had a broader distribution, also colonizing the large estuarine morph of *H. banksii.*

Despite both species being commonly associated with *H. banksii*, *L. undulata* prefers exposed environments (Grove 2017), which may explain the great abundance found on the east coast which is more exposed to wave action (Short 2006). Instead, *C. odontis* was more abundant on the sheltered north coast and in the estuaries suggesting that large scale environment factors likely contribute to their broad distribution and abundance. However, the response of gastropod species to different habitats may change also at small scales (centimetres, Beck et al. 1998; 2000), according to gastropod species characteristics (e.g. age, body-size, Crowe and Underwood 1999; Jones and Boulding 1999) and the differential ability of seaweed canopies (bioengineer potential) to provide favourable conditions beneath the canopies for associated species (Umanzor et al. 2017). These different conditions potentially create different niches that may select for certain gastropod phenotypes (Worthington and Fairweather 1989; Smoothey 2013). Thus, I further explored the spatial and temporal analysis of the shell size patterns of *L. undulata* and *C. odontis* (Chapter 3). Here, I provided evidence of variability in the shell morphology of the two species across habitats and regions where different *H. banksii* morphs occurred and suggested shell morphology may relate to specific environmental conditions and/or different *H. banksii* morphs (Jones and Boulding 1999).

Changes in gastropod shell size are indicative of differences in environmental conditions, such as wave exposure (Boulding 1993; Boulding et al. 1999) and extremes in temperature (McMahon 1990; Britton et al. 1995; Ansart and Vernon 2003; Stickle et al. 2016). Accordingly, our results highlighted a possible influence of environmental conditions on the shell morphology of each species, with *C. odontis* from wave-exposed sites having the largest foot and *L. undulata* from protected shores reaching the largest size. However, the differences in the shell morphology at small (site) and large (region and habitat) scales suggested an influence of seaweed morphology although, correlations resulted between *H. banksii* and shell morphology of *L. undulata* (20%) and *C. odontis* (18%) were relatively small. Different *H. banksii* traits, specifically thallus length and vesicles length contributed to the overall variation in the shell morphology of the two gastropod species according to the habitats where each *H. banksii* occurred. Likely, the bushy *H. banksii* morph provide additional protection to gastropod species with the high number of branches and vesicles, while on eastern shores, exposed to heavy wave action, the bigger vesicles of *H. banksii* provide a good surface for attachment gastropods, reducing the risk of dislodgement. These results reinforced a role for thallus structure in influencing the abundance and possibly shell morphology of gastropod species using the canopies as habitat (Chapman and Underwood 1994; Beck 1998, 2000; Kelaher 2003). However, to tease apart the effects of morphology and environmental conditions on engineering of the abiotic environment and gastropod abundance an experimental approach is required.

Seaweed morphology and density affect the bioengineer potential of canopy-forming seaweeds

To test the consistency of hypotheses from our mensurative studies, I used manipulative experiments to assess the role of *H. banksii* morphology and canopy cover on amelioration of key abiotic factors and gastropod abundance (Chapter 4). Transplant experiments are an

extremely useful tool to explore the adaptability of species to a new environment (Chapman 1986) and are required to determine the processes determining the structure of biotic communities (Underwood 1981; Paine 1994).

The transplant of fronds of the northern and eastern morph of *H. banksii* to one recipient site on the north coast of Tasmania, allowed us to test whether the standard (east) and small (north) morphs would differ in the ability to buffer temperature and irradiance and affect the colonization by gastropod in their natural environment. Despite no significant differences in temperature and light levels beneath the canopies of different *H. banksii* morphologies and cover, the canopies attenuated temperature by up to ~20% and light by ~80%, showing that as an ecosystem engineer, *H. banksii* has strong effects on temperature and light, providing shelter to species using the canopies as habitat.

Despite the evidence of a positive influence of morphology (Bates and DeWreede 2007) and density (Attrill et al. 2000; Parker et al. 2001; Cacabelos et al. 2007; Torres et al. 2015) on gastropod abundance, *H. banksii* morphology and density differently affected the colonization by the two dominant gastropod species. *Lunella undulata* was slightly more affected by *H. banksii* morphology and density, colonizing only the small morph and reaching the greatest abundance beneath the canopies with the greatest density. I attributed these patterns to a different habitat use by *L. undulata*, accordingly to differences in environmental conditions between regions. *Lunella undulata* from the north coast do not experience the same risk of dislodgement by waves compared to snails from the east coast but is instead exposed to a high risk of desiccation due the tidal regime of the north coast. Thus, the choice of *L. undulata* for the small over the standard *H. banksii* may be related to the capacity of the small *H. banksii* to retain water at low tide and reduce the high risk of desiccation caused by the semidiurnal tidal regime in this region (R. Lewis unpublished data), increasing the chances of survival of this species. As well, the presence of coralline turf on

which *L. undulata* feed (Worthington and Fairweather 1989) only occurred in the unmanipulated treatment and might also contribute to the absence of *L. undulata* beneath the standard transplants.

In comparison, *C. odontis* was affected by seaweed morphology and nearly density, occurring beneath the canopies of both the small and the standard morph and with an overall similar abundance among the different density treatments. Generally, canopy density has more positive than negative effects (Kelaher 2003) on the abundance of associated species, providing food (Duffy 1990; Viejo 1999) and a greater surface for colonization (Bishop et al. 2012). The lack of significant differences in temperature and light levels beneath canopies of different *H. banksii* morphs and cover, suggests the choice of *C. odontis* was influenced more by the amount of living space provided by each seaweed morph, accordingly to snail's size. Most of the *C. odontis* found beneath the eastern transplants and smaller *H. banksii* canopies were small recruits (~1 cm) and the high number of branches and vesicles may have provided a refuge from predators for these small individuals. However, since organismal-level response to stressful environmental conditions and habitat choice can differ both at spatial and temporal scales, due to fluctuations in environmental conditions, I further investigated the behaviour and habitat choice of *L. undulata* and *C. odontis* in the laboratory under controlled environmental conditions (Chapter 5).

Generally, field studies provide more 'ecologically relevant' observations on the importance of foundation species and environment factors on the habitat choice of associated species (Olabarria et al. 2002). However, laboratory experiments may be extremely useful to study species behaviour in a controlled environment and evaluate the importance of specific factors on the patterns observed in the field. However, the absence of "real" conditions could lead to a different species behaviour with respect the one observed in the field (Connell 1975; Chapman 2000), making hard to tease apart the effects of environmental factors (known and

unknown). Despite the constraints, we set up several choice laboratory experiments to evaluate the relative influence of seaweed morphology (habitat quality) and biomass (habitat quantity) on the habitat choice of gastropods, under different thermal conditions. In general, these lab experiments confirmed our findings in the field, although there were some exceptions.

In the choice experiments, the lack of exclusive colonization by gastropods of a specific *H. banksii* morph accordingly to the region of origin, was against the behavioural preferences for canopy-forming engineers found for other intertidal gastropods (Olabarria et al. 2002). Our results, considering also the ones from our observational studies, likely indicate that a fixed preference for a specific *H. banksii* morph does not exist despite the different abundance of species across habitats where different seaweed morphs occur. Thus, other factors, maybe species specific or external, may contribute to the observed patterns.

The two species showed a different response to temperature, accordingly to the region of origin, suggesting a local adaptation to the conditions present in the selected environment (Crowe and Underwood 1999). Intertidal gastropods from the north coast experience higher temperatures during daily low tide than the ones from the east coast and thus are likely to have a greater resistance against thermal stress which explain why both *L. undulata* and *C. odontis* did not often choose to colonize *H. banksii*.

Gastropods did not show a distinct habitat preference for different biomass of the two *H. banksii* morphs, with each species more affected by temperature. Most intertidal snails are freeze tolerant (Sinclair et al. 2004) but highly vulnerable to increasing temperatures (Chapperon and Seuront 2011). Warm temperatures are more likely to induce gastropods crawling (Newell 1958) and selection of habitats with the best conditions to maintain their body temperature (Soto and Bozinovic 1998) and the great colonization of the large *H. banksii* canopies by both *L. undulata* and *C. odontis* is consistent with this hypothesis.

However, the slight decreasing abundance of northern *C. odontis* and *L. undulata* within different biomasses of the small and standard *H. banksii* respectively, suggest an effect of habitat quantity on the choice of snails. The amount of living surface is known to affect the abundance of intertidal gastropods, but the effects are often specific to the habitat use of species (Beck 2000). The small *H. banksii* offer a great living surface to *C. odontis* often found attached on the vesicles and branches, while the standard seaweed morph provides a sheltered habitat to *L. undulata* beneath the canopies (Worthington and Fairweather 1989). Thus, these results support the hypothesis the habitat choice of intertidal gastropods may vary accordingly to the habitat use by each gastropod species and highlight an influence of *H. banksii* morphology and biomass, together with external temperature on these choices. Unfortunately, there is limited information available on the distribution of *L. undulata* across different habitats (Worthington and Fairweather 1989; Smoothey 2013) and even less for *C. odontis*, making it difficult to fully understand the factors which influence the behaviour and habitat choice of these species. Nevertheless, my results provided new data on the habitat choice of *L. undulata* and *C. odontis*, which together with our field results can provide the baseline for further studies of the factors influencing the choice of *H. banksii* as habitat. In addition, I showed that both species can survive well under artificial conditions and that a species-specific approach, combining both laboratory and field experiments, is necessary to avoid a generalization of the role of *H. banksii* as foundation species and ecosystem engineer.

Conclusions

The results presented in this thesis show variability in the structure of gastropod communities associated with different *H. banksii* morphologies. The small overlap in species between both habitats and regions where different seaweed morphs occur, indicate a different degree of adaptation by the single-species, while the differences in the abundance within the single habitat and region also indicate the possibility of small-scale adaptations to local

environmental conditions. As showed in the thesis, the mild role of *H. banksii* as an ecosystem engineer may change across habitats and with different environmental conditions. Specifically, despite the two *H. banksii* morphs buffered temperature and irradiance beneath the canopies at similar levels, they appear to provide habitat and protection for species beneath the canopies

Thus, assessing the role of intertidal seaweeds as ecosystem engineer by integrating field and laboratory experiments, being aware of the limit of working in an artificial environment, is likely to yield a bigger picture and greater insights of how a single species provides the foundation of entire communities. This kind of integrated approach will provide a better indication of the location-specific performance of intertidal seaweeds across habitats and help to understand the consequences of the disappearance of foundation species in a changing environment, allowing for better predictions of future condition of intertidal reefs in the face of global change.

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Appendix

Table A1: Geographical coordinates, wave exposure (based on Baardseth Index [BI] and air temperature (mean maximum and minimum for summer, spring and annual) 1998 to 2018 at each site. Abbreviations for sites as in Figure 2.1.

Site	Latitude	Longitude	Wave	Air Temperature					
			BI	Summer		Spring		Annual	
				Max	Min	Max	Min	Max	Min
GB	41°04’41.8” S	146°45’35.8” E	5.0	21.6	18.4	16.7	14.5	17.2	16.0
CP	41°60’42.4” S	146°48’18.9” E	7.0	21.6	18.4	16.7	14.5	17.2	16.0
GT	41°05’37.9” S	146°48’56.8” E	13.0	21.6	18.4	16.7	14.5	17.2	16.0
BBB	41°02’23.0” S	146°49’56.0” E	5.0	21.6	18.4	16.7	14.5	17.2	16.0
BC	41°01’22.0” S	146°56’39.0” E	12.0	21.6	18.4	16.7	14.5	17.2	16.0
F	41°30’50.2” S	148°16’39.0” E	0.0	24.4	19.7	19.2	15.8	18.8	17.3
FMC	41°33’25.5” S	148°17’33.6” E	6.0	24.4	19.7	19.2	15.8	18.8	17.3
SH	41°20’18.2” S	148°16’3.70” E	4.0	24.4	19.7	19.2	15.8	18.8	17.3
O	42°34’05.6” S	147°54’03.9” E	0.0	24.1	18.7	20.3	14.9	18.9	16.2
SB	42°34’0.50” S	147°53’17.5” E	16.0	24.1	18.7	20.3	14.9	18.9	16.2

Table A2: ANOVAs testing the effects of Habitat, Time and Site within habitat and time on individual morphological traits of *Hormosira banksii*. Analyses were based on transformed data (Box Cox transformation). Abbreviations: Ha: habitat; Re: region; Ti: time; Si: site; Res: residuals; Ha x Re x Ti(Si): the site is nested within the three main factors.

Response: Thallus Length

	Df	MS	F value	Pr(>F)
Ha	2	1.21	72.24	< 0.0001
Re	1	0.01	0.64	0.42
Ti	1	0.00	0.001	0.98
Ha x Ti	2	0.08	4.77	0.009
Re x Ti	1	0.02	1.31	0.25
Ha x Re x Ti(Si)	12	0.00	2.08	0.01
Res	220	0.00		

Response: Branches

	Df	MS	F value	Pr(>F)
Ha	2	0.04	22.97	< 0.0001
Re	1	0.24	122.08	< 0.0001
Ti	1	0.00	0.16	0.68
Ha x Ti	2	0.01	6.05	0.002
Re x Ti	1	0.02	10.37	0.001
Ha x Re x Ti(Si)	12	0.01	7.77	< 0.0001
Res	220	0.00		

Response: Vesicle

	Df	MS	F value	Pr(>F)
Ha	2	0.00	28.12	< 0.0001
Re	1	0.01	67.45	< 0.0001
Ti	1	0.00	12.83	< 0.0001
Ha x Ti	2	0.00	6.1	0.002
Re x Ti	1	0.00	5.98	0.01
Ha x Re x Ti(Si)	12	0.00	4.92	< 0.0001
Res	220	0.00		

Response: Vesicle Length

	Df	MS	F value	Pr(>F)
Ha	2	0.2	829.14	< 0.0001
Re	1	0.17	688.05	< 0.0001
Ti	1	0.02	110.34	< 0.0001
Ha x Ti	2	0.00	1.47	0.23
Re x Ti	1	0.01	52.1	< 0.0001
Ha x Re x Ti(Si)	12	0.00	13.13	< 0.0001
Res	220	0.00		

Response: Vesicle Width

	Df	MS	F value	Pr(>F)
Ha	2	0.14	565.74	< 0.0001
Re	1	0.14	538.73	< 0.0001
Ti	1	0.05	204.4	< 0.0001
Ha x Ti	2	0.00	0.88	0.41
Re x Ti	1	0.03	135.16	< 0.0001
Ha x Re x Ti(Si)	12	0.00	25.21	< 0.0001
Res	220	0.00		